AN INTRODUCTION TO ZOOLOGY

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AN INTRODUCTION TO ZOOLOGY

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PREFACE

This book has been written for the use of students taking the introductory course in Zoology in Universities and Colleges. It has been prepared especially for the zoological part of the work in General Biology at the University of Michigan, and is expected to supplement the one lecture and four hours of laboratory work per week during the first half year.

No textbook now on the market covers the field of the introductory course in Zoology as it is given at several of the leading Universities. These courses deal with invertebrate types only, being followed by a course on vertebrate types during the second half year. Only a few animals belonging to the more important phyla, as viewed from an evolutionary standpoint, are considered. They are, however, intensively studied in an endeavor to teach the fundamental principles of Zoology in a way that is not possible when a superficial examination of types from all the phyla is made. Furthermore, morphology is not specially emphasized, but is coordinated with physiology, ecology, and behavior, and serves to illustrate by a comparative study the probable course of evolution. The animals are not treated as inert objects for dissection, but as living organisms whose activities are of fundamental importance. No arguments, I believe, are necessary to justify this method of procedure, since the so-called "type course," developed with the problems of organic evolution in mind, and dealing with dynamic as well as static phenomena, is recognized by most teachers at the present time as the best method of introducing young students to Zoology.

The author has taught a course similar to that just outlined at the University of Wisconsin and to three successive classes at the

University of Michigan, and has based his presentation not alone upon his own experiences, but has profited by the experiences of other instructors with whom he worked.

No originality is claimed for this textbook. The material contained in it has been collected from many sources, and an attempt has been made to incorporate the results of the latest investigations. The majority of the figures have been borrowed from other textbooks and from original articles in scientific periodicals. The author is indebted to the Macmillan Company for the majority of these illustrations. He wishes also, to thank the following for the use of certain figures: Henry Holt and Co., 149–156; New Era Printing Co., 26, 62, 63; A. I. Root Co., 131, 147; Science Press, 91, 109, 110, 111, 116; United States Department of Agriculture, 135, 137, 141, 142; Wistar Institute of Anatomy and Biology, 12, 13, 25, 94. In every case the author's name follows the legend under the figures. Figures 1, 2, 3, 31, 49–51, 54, 123, and 157 were drawn by Mr. George M. Curtis under the author's direction.

The sources of information could not well be acknowledged directly, so the titles of the most important and easily accessible books and original articles have been arranged at the end of the book under the headings of the various chapters. The titles are numbered and are referred to by number in many places in the text. It is hoped that this list will be helpful to teachers, and that students may be encouraged to supplement their own observations and discoveries by consulting the original papers dealing with the topics under discussion.

In a first course in Zoology, students encounter a large number of scientific terms which cause them more or less confusion. For this reason a glossary has been included. It gives the meaning of the most important terms used, a key to their pronunciation, and shows their derivation.

In making acknowledgments it is necessary to explain that the present author planned the book with Dr. A. S. Pearse, and that the latter was to have prepared half of the manuscript

Lack of time, however, prevented him from completing his share of the work. Chapters I, II, and III were written by Dr. Pearse; Chapters I and II were then revised jointly, and Chapter III was completed by the present author alone. I wish to express my gratitude to Dr. Pearse for allowing me to use the first three chapters, for reading most of the remaining chapters, and for many valuable criticisms during the preparation of the manuscript.

In an endeavor to make the text as nearly correct as possible, the author sent the various chapters to specialists on the subject-matter treated therein. These gentlemen, however, are in no way responsible for any errors that may have escaped notice. The author is grateful to Professor Jacob Reighard for criticisms during the preparation of the work and for reading Chapter XIV, to Professor S. J. Holmes for reading the entire manuscript, to Rev. H. F. Hegner for reading Chapters I–VIII, to Professor C. M. Child for reading Chapters I–III, to Professor F. G. Novy and Dr. H. Hus for reading Chapters IV–VI, to Dr. O. P. Dellinger for reading Chapter IV, to Professor L. L. Woodruff for reading Chapter V, to Professor T. H. Montgomery, Jr., for reading Chapter VII, to Dr. E. R. Downing for reading Chapter VIII, to Professor W. C. Curtis for reading Chapter IX, to Professor J. Percy Moore for reading Chapter X, to Dr. A. E. Ortmann for reading Chapter XI, to Dr. E. F. Phillips and Mr. Max Peet for reading Chapter XII, and to Dr. A. G. Ruthven and Dr. H. Hus for reading Chapter XIV.

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JUNE 1, 1910.

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CHAPTER I

INTRODUCTION

1. Definitions

The science of *Biology* includes the sum of human knowledge with regard to organisms. That branch of biology which deals with animals is known as *Zoology;* that which relates to plants, as *Botany*. Zoology may be defined as the body of facts and doctrines derived from the scientific study of animals. Scientific study demands accurate and painstaking observation carried on with some definite end in view. The scientific study of zoology attempts to gain an understanding of the structure and activities of animals. It not only deals with the animals *per se,* but also with their relations to both the organic and inorganic worlds.

The detailed investigation of animals has led to the establishment of a number of subsidiary zoological sciences, several of which are briefly outlined in the next few paragraphs.

Systematic Zoology is concerned with the description of animal species and their arrangement according to a logical plan of classification. The exact meaning of the term *species* is a live question at the present time, and systematic zoologists do not agree as to what characteristics should be used in separating one species from another. One investigator in this field gives the following definition: "A species, as conceived by most systematists at the present time, may be defined as a group of interbreeding individuals which, while they may differ markedly among themselves, yet resemble each other more closely than they do those of any other group; the characters that distinguish the

group being considerable, not obliterated by intermediate forms, and inherited from generation to generation." Another prominent zoologist, when asked for a definition of a species, said it was "somebody's opinion." He did not mean that species are not realities in nature, but that just how many are represented in a particular group must usually be determined by competent authority.

Distributional Zoology attempts to ascertain the past and present habitats of animals, as well as the factors which control their distribution over the surface of the earth. The study of the distribution of recent animals is known as **Zoogeography**, and that of fossil forms constitutes a part of the science of **Paleontology.**

Animal Morphology is the science of form and structure. That part of it which pertains to the gross dissection of organs is known as **Anatomy**; that which relates to the microscopic study of tissues, as **Histology.** If, however, a study is concerned with the development of animals, organs, or tissues, it is included in the science of **Embryology.**

Animal Physiology deals with the functions of the parts of animals.

Animal Ecology is the study of the relationships of animals to one another and to their environment.

Evolutionary Zoology is concerned with the origin and descent of the different species of animals.

Paleozoology is the study of fossil remains of animals. It is intimately associated with all the other branches of zoological science, except the study of physiological processes. The physiology of extinct forms can only be inferred from the study of the activities of recent animals. Owing to the fact that fossils are usually embedded in stone, the mechanical appliances which are used in studying them are necessarily quite different from those employed in the investigation of modern animals.

The different branches of zoological science are closely related and mutually interdependent; for example, the students of evolution gain evidence concerning the ancestry of animals from

all the other fields of zoological investigation. From a careful examination of fossil forms, it is believed that the horse originated from a five-toed ancestor. This theory can be supported by evidence gained from the study of the embryology of modern horses. The physiology and ecology of horses give further evidence as to why some of the horse-like animals persisted to the present time, while others became extinct, and why horses are now found in some regions of the earth and not in others.

2. Classification

Animals are not infinitely variable. Their investigation has resulted in the establishment of about five hundred thousand species. These are grouped, according to similarity in structure, into about fifteen large divisions, or *Phyla*. One of the chief aims of zoologists in the past has been to give a complete descriptive inventory of the animal kingdom. The large number of species which have been described has made it necessary to separate each of the phyla into smaller and smaller subdivisions. Those animals which are most nearly related have therefore been placed together, and certain definite names are now generally adopted for use in classification. Thus under each phylum one or more *classes* are included, and under each class, a variable number of *orders*. In the following list of such terms the groups become successively smaller: *phylum*, *class*, *order*, *family*, *genus*, *species*, *individual*.

An example will perhaps make the system more clear. George Washington was an *individual;* he belonged, with other men, to the *species sapiens* of the *genus Homo*. This genus, together with another of somewhat questionable relationships, the extinct *Pithecanthropus*, constitutes the *family Hominidæ*. The *Hominidæ* are included with ten other families of monkey-like animals in the *order Primates*. Fifteen related orders, of which the *Primates* form one, are placed in the *class Mammalia*. All mammals possess hair and mammary glands; these characteristics dis-

tinguish them from the four other classes which make up the *phylum Vertebrata*, or animals possessing vertebral columns. The scientific name of any animal consists of the terms used to designate the genus and species; this is commonly followed by the name of the zoologist who wrote the first authoritative description of that particular species. The scientific name of man is therefore written *Homo sapiens* Linnæus.

The following concise synopsis of the chief groups of animals, together with a brief characterization of each of the fifteen phyla, will be of value to the student for subsequent reference. The terms used in describing these subdivisions will not perhaps be altogether understood by the beginner, but their meaning will be made apparent in succeeding chapters. It will suffice to say here that, in a general way, the classification of animals depends chiefly upon the characteristics which are contrasted in Table I.

TABLE I

CHIEF CHARACTERISTICS USED IN SEPARATING THE PHYLA OF ANIMALS CONTRASTED

1. Body composed of one microscopic unit, the cell.	Body composed of many cells.
2. Body formed from two primary cell layers, *i.e.* diploblastic.	Body formed from three primary cell layers, *i.e.* triploblastic.
3. Body radially symmetrical, *i.e.* parts (antimeres) radiating from a central axis.	Body bilaterally symmetrical, *i.e.* parts arranged in pairs on either side of a central plane.
4. Digestive cavity with only one opening.	Digestive cavity with two openings, the mouth and anus.
5. A cavity, the cœlom between the digestive tube and the body wall.	No cœlom present.
6. Body segmented, *i.e.* composed of a lineal series of parts, called metameres or somites.	Body unsegmented.

The figures following the diagnosis of each phylum indicate the number of recent species; those in parentheses, the number of fossil species known to represent it.

PRINCIPAL PHYLA OF ANIMAL KINGDOM[1]

1. **Protozoa.** — Single-celled animals; often colonial; sperm and egg cells usually wanting. 4400 (2000).

2. **Porifera.** — Sponges. Triploblastic (?); radially symmetrical, number of antimeres variable; body wall permeated by innumerable pores and usually supported by a skeleton of spicules. 600 (800).

3. **Cœlenterata.** — Jellyfishes, polyps, and corals. Diploblastic; radially symmetrical, with four or six antimeres; single gastro-vascular cavity; no anus; body wall contains peculiar bodies known as nematocysts or stinging cells. 3000 (1780).

4. **Ctenophora.** — Sea walnuts or comb jellies. Triploblastic; radial combined with bilateral symmetry; eight radially arranged rows of paddle plates; anus present. 1000 (no fossils).

5. **Platyhelminthes.** — Flat worms. Triploblastic; bilaterally symmetrical; single gastro-vascular cavity; no anus; presence of cœlom doubtful. 1600 (no fossils).

6. **Nemathelminthes.** — Round worms. Triploblastic; bilaterally symmetrical; possess a tubular digestive system with an anus; cœlom present. 1000 (no fossils).

7. **Rotatoria.** — Wheel animalcules. Triploblastic; bilaterally symmetrical; cœlom present; a pair of ciliated disks on the anterior end. 350 (no fossils).

8. **Bryozoa.** — Moss animals. Triploblastic; bilateral sym-

[1] Zoologists do not agree as to the number of phyla into which the animal kingdom should be divided. Some authorities recognize only eight, while others maintain that there should be as many as twenty, or even more. Two sub-kingdoms are generally recognized, *Protozoa* (Phylum 1) and *Metazoa* (Phyla 2–15). Recently many zoologists have come to believe that the sponges (Phylum 2) should be separated from other metazoons and called the *Parazoa*. The animals in Phyla 1–14 are usually called *invertebrates* to distinguish them from the *vertebrates* (15). Phyla 14 and 15, with a few animals of somewhat doubtful relationships, are commonly placed together under the group *Chordata*, and are known as chordates. Phyla 2–4 include animals without cœloms and are known as *Acœlomata* in contrast to phyla 5–15, which contain animals with a cœlom and are termed *Cœlomata*.

metry usually distorted by colonial habits; ciliated tentacles about the mouth; cœlom and anus present. 700 (1800).

9. **Brachiopoda.** — Tongue or lamp shells. Triploblastic; bilaterally symmetrical; cœlom present; anus present or absent; ciliated arms around the mouth; body covered by a shell composed of dorsal and ventral valves. 100 (2500).

10. **Echinodermata.** — Starfishes, sea cucumbers, sea urchins, sea lilies. Triploblastic; radially symmetrical, usually five antimeres; cœlom well developed; anus usually present; locomotion in many species accomplished by characteristic organs known as tube feet; a spiny skeleton of calcareous plates generally covers the body. 2500 (2600).

11. **Annelida.** — Jointed worms. Triploblastic; bilaterally symmetrical; cœlom well developed; anus present; segmented, somites similar. 2500 (25).

12. **Arthropoda.** — Crabs, insects, spiders, centipedes, scorpions, ticks. Triploblastic; bilaterally symmetrical; anus present; cœlom poorly developed; segmented, somites usually more or less dissimilar; paired jointed appendages present on all or a part of the somites; chitinous exoskeleton. 200,000 (5000).

13. **Mollusca.** — Clams, snails, devilfishes. Triploblastic; bilaterally symmetrical; anus and cœlom present; no segmentation; shell usually present; the characteristic organ is a ventral muscular foot. 22,000 (21,000).

14. **Tunicata.** — Sea squirts. Triploblastic; bilaterally symmetrical; cœlom and anus present; form saccular or barrel-shaped; two apertures through which water currents pass in and out; frequently colonial; all pass through a tadpole-like larval stage during which the body is supported by a rod-like structure, the chorda. 300 (no fossils).

15. **Vertebrata.** — Bilaterally symmetrical; cœlom well developed; anus present; chorda usually more or less fully replaced by a series of bony vertebræ; many systems of internal organs segmented; two pairs of appendages usually present; central nervous system always dorsal to digestive tube. 25,000 (2400).

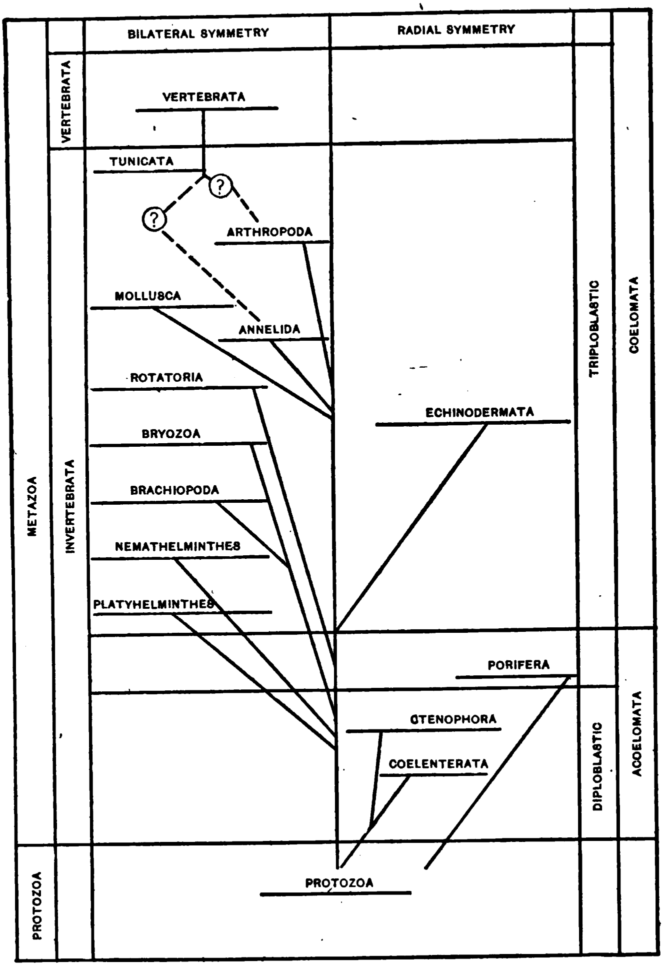


FIG. 1.

Figure 1 is intended to show the relationships of the different phyla of the animal kingdom to each other. The Protozoa are believed to have given rise to the other groups. The vertical height of each phylum upon the page represents the degree of structural specialization which it has attained.

CHAPTER II

PHENOMENA OF LIFE

I. Origin of Life

THOSE who are inclined toward the study of living organisms will find an abundance of material on every hand. Darwin raised five hundred and thirty-seven plants from three spoonfuls of mud which he scooped up at the edge of a pond. A recent naturalist has collected from four square feet of meadow over a thousand objects representing living animals or their remains. If we go to the depths of the sea, or to the tops of the mountains, or even penetrate the darkness of the caverns beneath the earth, we always find forms of animal life which have become adapted to almost every conceivable condition of existence.

The great abundance and rapid multiplication of living animals led the ancients to formulate some curious theories with regard to the origin of life. Even at this enlightened day it may be helpful to us to review some of their peculiar ideas. Many of the scholars of that period believed that every animal was originally created by divine providence. A favorite theory with those who did not accept this idea of *special creations*, was that of *spontaneous generation*. This was a universally accepted dogma from the time of the Greek philosopher Aristotle (384–322 B.C.) until 1668 when Redi overthrew it with his careful observations.

Ancient naturalists believed that frogs and toads arose from the muddy bottom of ponds under the influence of the sun, and that insects originated from dew. Those who did not accept these and other equally absurd views were subject to ridicule by their contemporaries. Before Redi performed his simple but remarkably effective experiments, no one had thought of testing the

verity of the theory of spontaneous generation. Redi proved conclusively that maggots never rise *de novo* from decaying flesh, as had been believed up to his time. He exposed meat in three jars under diverse conditions; one was left open, the second was covered with gauze, and the third was covered with parchment. The meat decayed in all of the jars, but maggots appeared only in the meat in the one which had been left entirely uncovered. Flies were attracted by the decaying meat in the second jar, but, being unable to enter, laid their eggs on the gauze, where they were found by Redi. No eggs were laid on the third jar, for the parchment did not allow odors to escape. By these and other experiments the theory of spontaneous generation fell into disrepute, but many of its adherents still maintained that even though some animals might not originate spontaneously, that fact did not preclude the possibility of others doing so.

Such dissenters made their last stand when the microscope revealed the swarms of minute animals which had been previously unknown. In one of their experiments hay was boiled in water until all the life had been killed; the liquid was then filtered off and placed in a tightly stoppered bottle. The subsequent appearance of a scum of living organisms in such infusions convinced them that life had arisen spontaneously. In 1775, Spallanzani proved that when proper precautions were observed no life developed in a culture of this kind. He prevented the entrance of air into the vessels containing the nutrient solution by hermetically sealing the slender necks of his flasks in flame. The flasks were then placed in boiling water for three quarters of an hour, all germs contained in them being destroyed. No life appeared in nutrient fluids thus treated. Despite this demonstration the question continued to be agitated for many years, and it was not until the time of Pasteur (1864) and Tyndall (1876) that the old theory of spontaneous generation was completely overthrown.

At the present time we are able to affirm that no living organism is known to originate except from some other preexisting

organism, and Preyer's aphorism "all life from life" is universally accepted. But though in the light of our present knowledge all are willing to admit the truth of this aphorism, there are those who hope that the advance of scientific knowledge may some time in the future enable us to clear up the problem of the beginnings of life which still remains unsolved.

2. Characteristics of Living Organisms

All the objects that come within the range of human experience may be grouped into two classes, living and non-living. Although our ideas concerning the origin of living organisms cannot go beyond the assertion that they always come from other living bodies, yet the characteristics that separate the two classes can be stated in a very definite way. Living organisms are characterized by (1) definite size, (2) definite form, (3) definite elementary composition, (4) definite organization, (5) growth by intussusception, (6) reproduction, and (7) irritability.

(1) **Size.** — If one were asked the question, Are organisms uniform in size? he would doubtless answer, No! but on more careful consideration it would become apparent that, although a wide range of variation exists, yet the differences in size are confined within rather definite limits. Certain parasites found in human blood, which can only be seen with the highest powers of the microscope, represent the smallest animals known; the whale is the largest. Although the discrepancy between these animals is enormous, yet the range of variation illustrated by them has a finite limit. On the other hand, the size variations of inorganic substances are infinite; for example, water is always recognizable as such whether it exists in the form of minute particles of vapor or reaches the dimensions of the Pacific Ocean. Although a wide range of variation occurs among animals in general, the individuals of any given species are practically equal in size. In many instances it is obvious that the size of a certain species fits it for the conditions under which it lives. The whale could not change places with one of the micro-organisms found in de-

caying matter. In a general way we may say that the structure and habitat of any animal limits its size.

(2) **Form.** — The various species of animals have characteristic forms by which they may as a rule be recognized. Many organisms are extremely irregular in form; for example, sponges incrust the surfaces of rocks or piles in an infinite variety of shapes, and no two trees of the same kind have a similar set of branches, yet every species has certain distinct peculiarities. A person who is familiar with sponges is able to recognize the different species at a glance, and any one can distinguish an oak from a poplar as far as he can see them.

Non-living bodies in most cases have no regularity of shape. A piece of granite may form a slab or a boulder or assume any other contour; the water in a lake conforms to the shape of the lake-bed.

(3) **Chemical Composition.** — If a sufficient variety of inorganic bodies are collected and analyzed, every one of the eighty or more chemical elements known to science will be represented. If, on the other hand, any number of living organisms are collected, generally not more than twelve elements can be secured by analysis. Furthermore, only five of these will usually be represented in considerable quantities. Thus a typical animal would be found to contain the following elements: —

Carbon Oxygen Nitrogen Hydrogen Sulphur	99 per cent of weight;
Phosphorus Chlorine Potassium Sodium Magnesium Calcium Iron	1 per cent of weight.

The elements constituting living substance, form complex organic compounds which exhibit three striking peculiarities: (1) they are in most cases labile substances, *i.e.* they are unstable and may be broken up into simple compounds, or synthesized into more complex molecules, (2) carbon is always an important constituent, and (3) their important elements are all non-metallic.

The chemical composition of living matter is highly variable. A complete analysis of representatives of any two species would never give identical results; and even young and old individuals of the same species would not agree. Nevertheless, all animals show a remarkable uniformity in chemical composition. Some animals might be considered exceptions to this general rule; for example, a clam upon analysis would show a large percentage of calcium carbonate owing to the presence of that salt in its shell. The shell, however, is really not a part of the living substance, but represents an inorganic accretion that has formed around the body.

(4) **Organization.** — Although living organisms exhibit great diversity in structure, a careful examination of all the parts proves that the fundamental elements are essentially the same in every individual. All plants and animals are composed of similar microscopic units, called *cells*, which are arranged in a characteristic manner for each species. Thus the body of a very simple organism may consist of only a single cell, whereas that of a complex organism may contain billions. Cells may be compared with bricks which are used to build houses. Bricks may show variations in form, color, and composition, but have certain characteristics which make them easily recognizable whether they are separate or built into walls. In a similar way, though individual cells show minor differences, they agree in fundamental characteristics, and may readily be identified, even when constituents of a many-celled animal.

Whether an organism is unicellular or multicellular, it always consists of a number of unlike parts which are incapable of inde-

pendent existence. When the essential parts of a living animal are separated from one another, they soon lose their identity and ultimately disintegrate into simple inorganic compounds. Non-living bodies have no common unit of structure which is comparable to the cell, and their parts show no interdependence.

(5) **Growth** in living organisms is usually by *intussusception*, *i.e.* by the addition of new particles among those already present; this results in a swelling of every part, and does not necessitate a change in form. Non-living bodies usually grow by *accretion*, *i.e.* the addition of successive layers on the outside.

Growth in any living thing involves a complex series of changes. The chemical compounds which make up the bodies of animals are extremely labile; they are constantly breaking down into simpler substances or becoming more complex by the addition of new materials. There is no time during the life of any individual when elaborate chemical reactions are not taking place. **Metabolism** is the term used to include this great complex of incessant changes. Those processes which use energy to build up compounds are said to be *anabolic;* those which destroy substance to produce energy are termed *katabolic.*

Animals are primarily katabolic organisms. They cannot make organic compounds from simple inorganic substances; in this respect they differ from plants which manufacture starch from carbon dioxide and water. Since animals must have organic food, it follows that plant products are necessary. Before animal growth is possible, food must be converted into living substance. By the process of digestion food is prepared for absorption. Some substances that cannot be digested are passed out of the body as *fæces.* After absorption, food is carried to some part of the body where it is needed; here it is transformed into living substance by the process of *assimilation.*

In order that metabolic activity may go on without ceasing, a constant supply of energy is necessary. This energy is in part furnished by *oxidation*, *i.e.* the chemical union of oxygen with the living substance in a manner which may be compared to the

changes taking place during combustion. *Respiration* supplies the oxygen for such metabolic activities, and also eliminates certain gaseous excretory products. The waste products formed by the breaking down of living substance are cast off as *excretions*. These should not be confused with fæces, which have never actually become constituents of living matter.

Figure 2 is intended to indicate the relations of the various metabolic activities. It shows that an animal requires food and

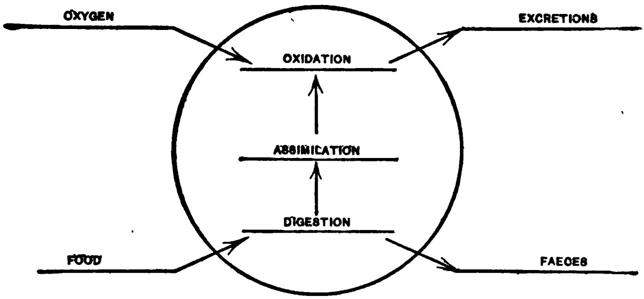


FIG. 2. Diagram showing the relations of the various metabolic activities of animals.

oxygen; that part of the food is digested and assimilated, while the rest is cast out as fæces; and that the oxidation of the living substance results in the production of certain excretions which are eliminated. *Urea* is the most important of these excretory products.

Growth has been said to represent the excess of anabolism over katabolism. The power of growth becomes gradually less throughout the life of any individual, and all animals pass through certain well-marked stages, youth, maturity, and old age. *Youth* is generally characterized by great vigor and activity as well as rapid growth. At *maturity* anabolism and katabolism are about equally balanced. During this adult period little change is observable in external form or gross weight. Maturity gradually gives way to *old age*, a period of decline, when the body

slowly wastes away and the vital processes finally cease altogether. These three periods, youth, maturity, and old age make up the *life cycle* of every individual.

(6) **Reproduction.** — Perhaps the most remarkable characteristic of a living organism is its ability to produce new individuals like itself at some time in the life cycle. This reproductive power usually manifests itself during maturity. Among animals an offspring may originate from its parent by asexual or sexual methods. Reproduction may take place by a splitting of the entire body into two or more parts, each of which takes up an independent existence. This method of multiplication is often called *asexual reproduction;* if the new individuals are formed by a division of the original or parent body into approximately equal parts, reproduction is said to be by *fission;* if, on the other hand, only a small portion of the parent individual becomes separated as a distinct organism, reproduction is by *budding*, and the offspring are called buds. Sometimes an animal passes through a resting stage during which the body fragments into a large number of small parts which subsequently become free individuals. This asexual method of reproduction is known as *sporulation.*

Sexual reproduction involves the union of substances from two different animals. When this process occurs in certain one-celled animals, two individuals come together and exchange a portion of their living substance (Fig. 31); in many-celled animals there is a union of sexual cells, *egg* and *sperm*, which originate from two separate individuals. Asexual reproduction increases the number of individuals without altering the nature of their substance; sexual reproduction originates new individuals by mixing portions of two preexisting organisms.

Asexual reproduction may be illustrated by *Paramecium* (p. 67), a single-celled animal which divides twice during every twenty-four hours when conditions are favorable. Its metabolism is so rapid that it can grow to its maximum size in half that period of time. The honey bee (Chap. XII) furnishes an excellent illustration of *sexual reproduction.* Three sorts of bees exist: the

workers, which are sterile females and take no part in reproduction; queens, or sexually mature *females;* and drones, or *males.* New individuals are formed by the fusion of reproductive or *germ cells.* The drone injects the sperm cells into the queen, where they are stored up to unite with the egg cells as they ripen within her body.

(7) **Irritability** or **reactiveness** is a characteristic property of organisms. It gives them the power to respond to changes in their environment in such a way that they usually attain favorable conditions for existence. Any change in conditions that produces the reactions of an animal is termed a *stimulus.* Stimuli may be external or internal; the former includes changes in temperature or light, in the composition of the surrounding medium, etc.; hunger and fatigue may serve as examples of internal stimuli.

In many instances animals show very uniform responses to stimuli. An excellent illustration of this fact is furnished by the katydid. The relation between the temperature and the number of calls per minute is so constant in this insect that the exact atmospheric temperature may be computed from the following formula.

$$\text{Temperature} = 60 + \frac{\text{no. of calls per minute} - 19}{3}$$

The *adaptive power* of animals may be further illustrated by the kidneys of man. In man, as in all vertebrates, these are paired organs occupying a position near the dorsal side of the body wall. Under normal conditions both eliminate an approximately equal amount of excretory matter. However, no permanent injury necessarily results if one is removed, for the kidney on the uninjured side of the body enlarges to such an extent that it is able to carry on the functions previously performed by both.

Instances of this adaptive power might easily be multiplied, for they are common everywhere. In a broad sense, even the intelligence of man and the degree of success he may attain depend upon how successfully his reactions meet surrounding conditions.

3. Plants and Animals Compared

It is easy to choose characteristics that will serve to distinguish a tree from a man, but the separation of the simplest animals from the simplest plants is a more difficult problem. In fact, there are at the present time a number of organisms that are claimed by both botanists and zoologists. There is no single peculiarity which can be used in all cases to discriminate between these groups of organisms. The view now generally accepted is that plants and animals originated together but have developed along divergent lines. However, certain general features can be indicated in which the two kingdoms differ. These are given in the following table; but the reader should bear in mind that there are exceptions to every one of these criteria.

TABLE II

CHIEF CHARACTERISTICS OF PLANTS AND ANIMALS CONTRASTED

	Plants	Animals
1. Structure	Form of body rather variable; new organs added externally.	Form of body usually invariable; organs compact and mostly internal.
2. Locomotion	Usually none in adult condition.	Usually well developed.
3. Irritability	Respond to stimuli slowly; no nervous system.	Respond to stimuli quickly; nervous system present in higher forms.
4 Metabolism	Possess chlorophyll; manufacture organic food from CO_2 and H_2O in the presence of light.	No chlorophyll; require organic food.
5. Waste products	Oxygen, carbon dioxide, water.	Carbon dioxide, water, urea, fæces.

The presence of chlorophyll in green plants has an important bearing on metabolism, for it enables plants to manufacture starch when light is available. This simple organic compound is

built from the inorganic substances, carbon dioxide and water. With starch as a basis more complex organic compounds are elaborated by the living substances. Now the living substance of plants is practically the same as that of animals, and it seems strange at first thought that plants should give off oxygen as a waste product, for this gas is one of the constant needs of living substance. If, however, we keep in mind the fact that chlorophyll is carrying on one set of processes (Fig. 3) which require

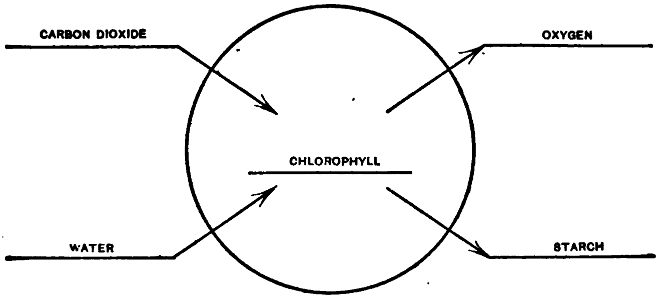


FIG. 3. Diagram showing the activities of chlorophyll.

carbon dioxide and liberate oxygen as a waste product, while the living substance is carrying on another set which use oxygen and release carbon dioxide (Fig. 2), the matter becomes one of simple addition and subtraction; one group of processes uses the waste products of the other.

The qualities that are usually cited as being peculiarly characteristic of animals are *locomotion* and *nervous activity*. With the exception of a few extremely sensitive species of which the common sensitive plant, *Mimosa pudica*, is the most familiar example, plants respond very slowly to external stimuli and their power of transmitting impulses is poorly developed. Locomotion is absent except in a few simple forms and free swimming reproductive cells.

4. The Physical Basis of Life: Protoplasm

When the biologists of the past century turned their microscopes upon the swarms of simpler plants and animals or examined the tissues of multicellular organisms, they saw the remarkable substance that forms the physical basis for all the activities of living organisms without realizing its importance. Felix Dujardin, in 1835, first clearly distinguished this substance from other viscid matter and called it "sarcode." Later investigators made more extended studies, but Dujardin's term was not generally adopted. Sarcode was believed to be generally present in the simple animals, but a different substance, called *protoplasm*, was thought to be the living element in the complex organisms. Max Schultze, in 1861, convinced the scientific world that the living substance in both simple and complex plants and animals is practically identical in structure, composition, and physiological properties. The term "protoplasm" adopted at that time has persisted to the present day.

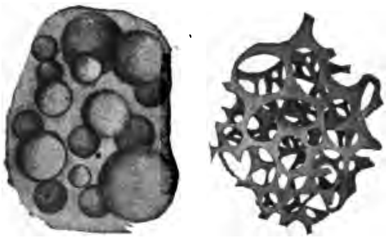
Schultz's generalizations were of vast importance and gave a great impetus to the study of fundamental problems. Huxley called protoplasm the *physical basis of life*, a peculiarly expressive phrase, since in protoplasm lies the ultimate explanation of all vital phenomena. It is fitting, therefore, in this connection to consider more fully the properties of living substance.

Protoplasm is subject to all the physical laws of fluids. It exhibits currents and flowing movements, and is influenced by changes in surface tension. Its specific gravity is always a trifle greater than that of water. It is usually entirely colorless or gray. On account of its importance, the minute structure of this living jelly has long been a favorite field for study in both plants and animals. Protoplasm has been repeatedly examined under the very highest powers of the microscope. Elaborate methods have been devised for preserving it so that its structure may be similar to that which existed during life. Many theories have been advocated with regard to the finer

structure of protoplasm. Of these the three following may be mentioned.

(1) The *Reticular Theory* maintains that protoplasm consists of a living network of anastomosing fibers (Fig. 4, B); between these a variety of non-living substances, such as water and fat, may be present.

(2) The *Alveolar Theory* (Bütschli, 1892) supposes that protoplasm has a foam-like structure somewhat similar to a mass of minute droplets such as exist in an emulsion of oil and water (Fig. 4, A). The originator of this theory was able to make artificial emulsions which showed a striking resemblance to living substance. He maintained that the fibrous network, described by the adherents of the reticular theory, represented the walls of the alveolar bodies which had been cut across.



A B

FIG. 4. Diagrams illustrating (A) the alveolar, and (B) the reticular theory of protoplasmic structure. (From Dahlgren and Kepner.)

(3) The *Granular Theory* (Altman, 1892) asserts that protoplasm is composed of innumerable living granules arranged either along fibers or among alveoli; nothing is essential, however, except the granules.

None of these theories has universal approval, but the first two have been more widely accepted than the last. Many recent authorities believe that protoplasm is highly variable in structure. A fourth view held by many observers is "that the various types described above are connected by intermediate gradations and may be transformed one into another" (19, p. 27).

Protoplasm is a mixture of extremely complex chemical compounds; these are, at least in part, extremely labile and therefore are apt to vary at different times. It is impossible to study living substance, since even the most careful methods of analysis

immediately kill protoplasm. "Hence ideas upon the chemistry of the living object can be obtained only by deductions from chemical discoveries in the dead object" (17, p. 102). Nevertheless, we have gained a considerable amount of knowledge as to the chemical nature of protoplasm. Ninety-seven per cent of the organic and inorganic constituents of protoplasm are made up of four elements, occurring in the following proportions:—

Oxygen	65 per cent
Carbon	18.5 per cent
Hydrogen	11 per cent
Nitrogen	2.5 per cent

These and other less important elements form certain rather definite groups of compounds, which we will now consider in some detail.

Water is the most important of the inorganic constituents; it comprises more than 50 per cent of the weight of most animals, and in some marine forms reaches as high as 99 per cent. It seems remarkable that man is able to exist when 59 per cent of his body is made up of water. It not only occurs in combinations, but also acts as a solvent for various substances that are found in protoplasm.

Aside from water the most important inorganic substances are various *salts* and dissolved *gases*. Of the salts the chlorides, carbonates, and phosphates of the commoner alkali and alkali-earth metals predominate. The principal gases are carbon dioxide and oxygen.

The organic compounds found in protoplasm are divided into three general classes: proteids, carbohydrates, and fats. "Of these only the proteids and their derivatives have been demonstrated with certainty as common to all cells; hence, they must be set apart among the organic constituents of living matter as the essential or general substances, in contrast to all special substances" (17, p. 103).

Proteids are always composed of the five elements, carbon,

oxygen, hydrogen and nitrogen, and a small amount of sulphur. In this respect they differ from the other two classes of organic compounds which lack the nitrogen and sulphur. The proteid molecules are extremely large, one often containing more than a thousand atoms. They are not readily diffusible through animal membranes, this being due in part to the size of the molecules and also to the fact that such complex compounds do not dissolve completely unless they break down into simple substances. Instead of dissolving, proteids absorb enormous quantities of water, swelling up like a sponge; they are called *colloids* to distinguish them from *crystalloids*, like sugar, which are easily soluble. *Coagulation*, or clotting, is another peculiarity of proteids.

Carbohydrates are compounds of carbon, hydrogen, and oxygen, the last two always occurring in the same proportions in which they are found in water (H_2O). The most familiar examples of this class of substances are the starches and sugars, which are characteristic of plants rather than animals, though found in both. Carbohydrates are comparatively simple compounds when contrasted with the proteids, and are readily oxidizable, thus producing energy. Some varieties of living substance apparently contain no carbohydrates.

Fats, likewise, are not invariable constituents of protoplasm. Though of widespread occurrence, fatty compounds are particularly characteristic of animals. They may be said to consist of an alcohol (glycerin) which has lost some water and combined with a fatty acid. They are all lighter than water, and do not unite with it.

Protoplasm consists, then, of complex and variable mixtures of proteids, carbohydrates, and fats, together with water, salts, and dissolved gases. No uniform chemical formula can be given for it; in fact, one of its chief characteristics lies in the unceasing changes that it undergoes. It has the properties of metabolic activity, irritability, contractility, reproduction, and all others peculiar to living organisms (p. 10). It seems strange that such

a changeable substance should possess great specificity, yet such is the case. The protoplasm of each species of organism is perfectly distinct from that of every other species. A tree of a certain variety always gives rise to other trees similar to it; for example, a pear seed never develops into a peach tree, but always into a pear tree of the same kind that produced it; likewise the egg of a pure-bred Plymouth Rock hen never gives rise to anything but a chicken of the Plymouth Rock variety. Nevertheless, both the tree and the hen take their origin from an apparently simple microscopic bit of protoplasm, the fertilized germ cell.

5. A Physico-Chemical Explanation of the Phenomena of Life

The efforts of the alchemist of old who wrought in the seclusion of his laboratory were directed toward the solution of two problems: the production of an elixir of life, and the manufacture of gold. His time has passed, and his problems were never solved. His successor of modern times, the biochemist, has likewise chosen problems of fundamental importance and great difficulty; he has attempted to give an explanation of all vital phenomena by means of physical and chemical laws. The scientific world now contains many scholars who maintain that living organisms are really *machines*, and are opposed to the idea of *vitalism*, which presupposes the presence of some vital principle. One of the leading investigators in this field claims that living organisms are to be considered as "chemical machines, consisting essentially of colloidal material, which possess the peculiarities of automatically developing, preserving, and reproducing themselves" (15, p. 1). Another prominent zoologist makes the following statement: "I say again, with all possible emphasis, that the mechanistic hypothesis or machine theory of living beings is not fully established, that it *may* not be adequate or even true; yet I can only believe that until every other possibility has really been

exhausted, scientific biologists should hold fast to the working program that has created the sciences of biology. The vitalistic hypothesis may be held, and is held, as a matter of faith; but we cannot call it science without misuse of the word" (20, p. 21). A great many scientists have recently come forward to combat the old idea of vitalism, and, though some of them have made errors, their influence as a whole has been highly stimulating to zoological thought.

Until comparatively recent times it was believed that organic compounds could be built up only by living substance. Even such an able scientist as Liebig supposed that his beef extract contained some vitalistic principle that was imparted to those who ate it. His ideas were overthrown by a simple experiment. Six puppies from the same litter were divided into two lots; three were fed beef extract and the others were allowed to remain without any food whatever. Those fed with the beef extract died first, thus demonstrating that the extract was more a stimulant than a food. The belief that organic compounds could only come from living organisms was proven erroneous as early as 1828, when Woehler made urea by a synthetic process in his laboratory. It was to combat such *vitalistic* ideas that the "*mechanistic*" *theory* first arose, and its adherents have met with a considerable degree of success. Experiments from many sources might be cited which support the mechanistic view, but only a few selected instances can be given.

Many organs will carry on their normal activities when removed from an animal's body. A turtle's heart will remain alive and beat for a couple of days if it is placed in a dish containing a proper mixture of mineral salts in water. Furthermore, the rate of the beats may be increased or decreased at the will of the experimenter by varying the proportionate amounts of the salts in solution.

Organs from one animal may be grafted upon another. There is a gland, the thyroid, in the neck of human beings, which, when diseased, causes a malady known as goiter. The removal of the

thyroid is followed by death. It was discovered some time ago that this gland might be removed with impunity if a piece of a healthy gland from another animal, such as a sheep, were grafted under the skin in any part of the body. The foreign piece of tissue appropriates a blood supply and becomes functional in its new position. This is one of the many cases proving that a definite positional relation of organs is not always necessary if their secretions are present.

The opponents of vitalism have also brought forward many arguments against that theory from a study of *enzymes* or *ferments*, a class of substances which cause chemical reactions without undergoing any change themselves. An example is ptyalin, which is present in human saliva and has for its function the change of starch to sugar. A large number of substances of this sort are known to be present in living organisms. The explanation of their actions makes clear many processes which were formerly supposed to be due to certain vitalistic principles. Research in this field is only in its infancy.

These instances are sufficient to show that the mechanistic point of view is a much more progressive one than the vitalistic. Through its influence scientists have been able to prove that a large number of the activities present in living matter are subject to definite laws, many of which have been known for a long time to physicists and chemists. However, this method has not explained all vital phenomena, and perhaps never will.

CHAPTER III

THE CELL AND THE CELL THEORY

1. Morphology and Physiology of Cells

The protoplasm contained in the body of an animal is not one continuous mass, but is separated by membranes and other structures into a great number of minute bodies called *cells*. These cells, though varying greatly in size and shape, all have the same fundamental plan of structure. The simplest animals consist of a single cell, but the bodies of the more complex forms are made up of millions of these tiny bits of protoplasm. On account of its universal presence in animals and plants, the cell has been called the *unit of life*. It is necessarily of vast importance in the solution of biological problems, and has been much studied by investigators during the past forty years.

In order to have the structure of a typical cell clearly in mind we will now turn our attention to the following description of its parts. Reference to Figure 5 will make the written description clearer. Since the cell contains protoplasm, which acts like a fluid, it naturally tends to have a spherical form. This condition is seldom realized in nature, for various factors, such as unequal growth and pressure from other cells, modify the shape. The fact that the cell shown in the figure has an oblong outline is, therefore, of no significance.

The contents of many cells includes not only the active protoplasm, but also various kinds of passive bodies such as fat globules. These are known as *metaplasm*. The *protoplasm* of any cell is made up of two principal kinds of substance, the *cytoplasm* and the *karyoplasm*. The *nucleus* contains all of the latter. It is the central body, and is, for various reasons, regarded as the

controlling organ of cell activities. A distinct though delicate *membrane* usually separates it from the surrounding cytoplasm. The ground substance of the nucleus is a sort of sap, called *nucleoplasm*, through which runs a network of thin *linin fibers*. The most important nuclear constituent is the *chromatin*, a substance that has a strong affinity for certain dyes. Chromatin

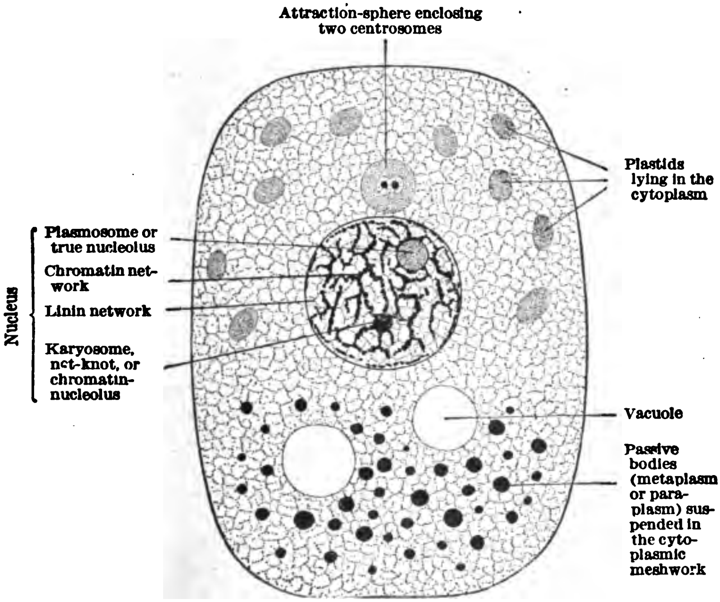


FIG. 5. Diagram of a cell. (From Wilson.)

is generally arranged in the form of a more or less irregular network of granules which are scattered about on the linin fibers. Frequently several granules unite to form a net knot or *karyosome*. In addition to these regular constituents of the nucleus, one or more bodies, known as *nucleoli*, may be present. Although cells usually contain only one nucleus, two or more may occur in certain cases.

Cytoplasm always surrounds the nucleus. It is sometimes

arranged in concentric zones, each containing a different kind of protoplasm; or it may be modified to form hair-like projections called cilia, and other cellular organs. The structure of cytoplasm is, however, rather uniform in the same cell, but highly variable in different cells, and sometimes even in different stages of an individual cell. A careful examination of certain cells appears to leave no doubt but that a reticular network is present in the cytoplasm. Other cells show no sign of such an arrangement of materials. The alveolar condition exhibited by many cells is perhaps the most typical.

Although a definite *cell wall* is more often found in plants than in animals, the cytoplasm of the latter may secrete a delicate membrane, or even a wall of considerable thickness, as in the case of cartilage (Fig. 48, C).

Embedded in the cytoplasm, usually near the nucleus, is a minute but important body, the *centrosome*, or a pair close together. The centrosomes are often surrounded by a clear space, the *centrosphere*. Among the other bodies suspended in the cytoplasm may be mentioned oil and *water vacuoles*, *crystals*, and certain organs known as *plastids*. Plastids may be colored (chromoplastids) or white (leucoplastids).

There is a definite division of labor among the parts of a cell. The particular function of the *nucleus*, aside from its important relation to cell division, to be described later, seems to be the control of the activities by which the protoplasm is elaborated.

The *cytoplasm*, from its direct relation to the outside world, is the seat of such functions as irritability, absorption, digestion, excretion, and respiration. The *centrosome* is of importance during cell division. The *cell covering* may be secreted for protection or support, or may be extremely delicate and have significance only as it helps to control the absorption of certain fluids. *Plastids* may represent stored food or waste products; some of them, however, have other functions, *e.g.*, the *chloroplasts*, which carry on *photosynthesis* in many plant and a few animal cells.

As has already been noted, the *size* and *form* of cells are variable. Bacteria are among the smallest known, some of them measuring not more than one hundred thousandth of a meter in length. On the other hand, the eggs of a large bird are single cells; they are exceeded in length by certain nerve cells whose fibers extend out almost a meter. The limit in size is probably determined by the nucleus, since it regulates the metabolic activities of the cell.

Some idea of the wide variation in the form of cells may also be gained from Figure 48, which shows specimens of various types.

All of the life processes of the simplest animals, the Protozoa, are carried on by a single cell. The cells of a multicellular animal, a Metazoon, are mutually dependent, and cannot exist if isolated. In many cases there is actual continuity between the protoplasm of different cells, and some zoologists have gone so far as to maintain that the body of a complex animal should not be considered an assemblage of separate cells, but a continuous mass of protoplasm with nuclei scattered through it. Often this connection between cells is brought about by slender protoplasmic bridges (Fig. 46, C); in other instances cells are so indistinguishably blended that no boundaries can be discerned. A cell is therefore not always a true "unit," but a necessary part in a complex whole. The number of cells associated to form a single organ is often enormous; the number of nerve cells in the gray matter of the human brain has been estimated at 9,200,000,000; all of these together would occupy only a trifle more than a cubic inch of space.

2. Cell Division

Cells multiply either by direct or indirect division. *Indirect cell division* always involves a definite series of stages which follow each other in a regular sequence, the whole process being known as *mitosis*, or mitotic cell division. *Direct division* or *amitosis*, is a more simple process having no complex series of stages.

(1) **Mitosis.** — A cell that is not undergoing division is said to be in a resting condition (Fig. 6, A). When it divides by the indirect method, the series of changes may conveniently be arranged in four stages, known as the *prophase*, *metaphase*, *anaphase*, and *telophase*. The modifications occurring during mitosis are primarily concerned with the nucleus and centrosomes, the cytoplasm remaining comparatively passive.

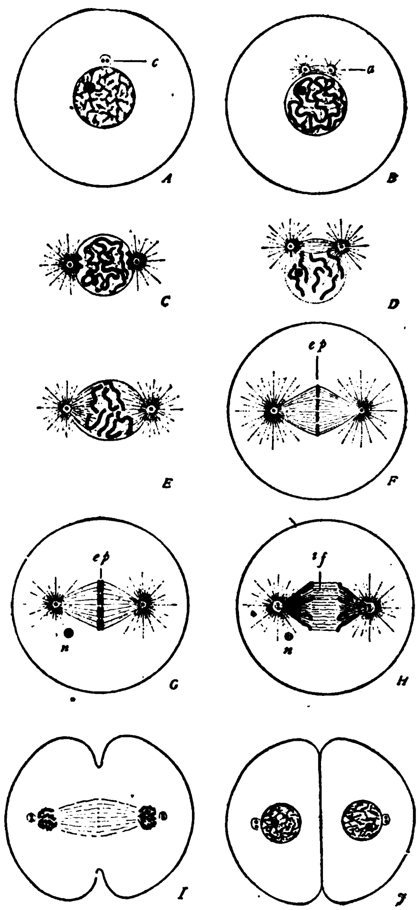


FIG. 6. Diagrams illustrating mitotic cell division. (From Wilson.)

The *prophase* is characterized by preparatory changes. The chromatin granules that are scattered through the nucleus in the resting cell become arranged in the form of a long thread or *spireme* (Fig. 6, B). At the same time the centrosomes move apart, finally reaching opposite sides of the nucleus (B, C, D, E). The radiating lines that appear about them (B) later give rise to a *spindle* (D). While this is going on the nuclear membrane generally disintegrates and the spireme segments into a number of bodies called *chromosomes* (D); these take a position at the equator of the spindle,

halfway between the centrosomes (E). The stage shown in Figure 6, F, is known as the *amphiaster;* at this time all of the machinery concerned in mitosis is present. There are two *asters*, each consisting of a centrosome surrounded by a number of radiating *astral rays*, and a spindle which lies between them. The chromosomes lie in the *equatorial plate* (*ep*).

During the second stage, the *metaphase*, the chromosomes split in such a way that each of their parts contains an equal amount of chromatin (G). As we shall see later, this is one of the most significant events that takes place during mitosis. Often the chromosomes split before they have assumed an equatorial position (Fig. 6, E); other minor variations also occur.

During the *anaphase* (Fig. 6, H), the chromosomes formed by splitting move along the spindle fibers to the centrosomes. As a result every chromosome present at the end of the prophase (F) sends half of its chromatin to either end of the spindle. The mechanism that brings about this migration is as yet somewhat in question. Fibers are usually left between the separating chromosomes; these are known as *interzonal-fibers* (H, *if*).

The *telophase* (Fig. 6, I, J) is a stage of reconstruction from which the nuclei emerge in a resting condition; the chromatin becomes scattered throughout the nucleus, which is again enveloped by a definite membrane (J); the centrosome divides and, with the centrosphere, takes a position near the nucleus. Finally the cycle is completed by the constriction of the cell into two daughter cells (I, J) each of which is in condition to carry on the regular metabolic processes until it in turn becomes ready to divide.

The *origin of the structures* that take an active part in mitosis is not definitely known. Only the *centrosomes* are represented in the resting cell; these usually arise from the division of preexisting centrosomes, but in certain cases they are wholly absent (higher plants), or their existence is questionable (Protozoa). The *chromosomes* are formed directly by a condensation of chromatin. The origin of the *spindle fibers* is variable. Sometimes

they are formed from the cytoplasm, and sometimes they arise from the linin network in the nucleus. Linin does not, however, differ greatly in chemical composition from the cytoplasmic substance, and the spindle fibers are, therefore, always composed of *achromatic* material. The *nucleolus* is apparently of no importance in mitosis; it degenerates during the early stages (Fig. 6, G, H, *n*) and is reformed during the telophase (J). The two cells that result from mitosis may be equal (J) or unequal in size. The division of the cytoplasm appears to be of little importance, but with rare exceptions there seems to be an equal division of chromatin; this is apparently the essential process.

Under ordinary conditions every animal develops from a single cell, and, since the chromatin persists from one cell generation to another, the chromosomes are considered by most zoologists to be the *bearers of hereditary qualities* from parent to offspring. Every species of animal has a definite number of chromosomes that appear when the cells of its body undergo mitosis. Thus sixteen are characteristic of the cells of oxen, guinea pigs, and man; the grasshopper has twelve; the brine shrimp (*Artemia*), one hundred and sixty eight; the round worm (*Ascaris*), four or two. The last example illustrates one of the unusual cases in which two individuals that are mutually fertile have a different number of chromosomes. An even number of chromosomes is characteristic of most animals, but recent researches have demonstrated that some forms, particularly the males of insects, have an odd number.

(2) **Amitosis.** — Although mitosis is considered the typical method of cell division, the multiplication of nuclei by direct division or *amitosis* is not uncommon. This process (Fig. 7) does not have such a definite series of stages as mitosis, and is much simpler. The nucleus elongates, and the nucleolus divides, one half passing to either end of the nucleus. Sometimes the nucleolus remains at one end, a new one being formed at the opposite end. The nucleus divides by one of three methods: (*a*) often the nucleus is pinched in two in the middle, or (*b*) a

plate is formed at the plane of division which later becomes double, and then the two plates separate, or (*c*) two nuclear membranes are built up inside of the old membrane, which then breaks down, allowing the daughter nuclei to escape.

"The cell body is the last to divide in amitosis, and in many, perhaps the majority of cases, it does not do so at all" (21, p. 38).

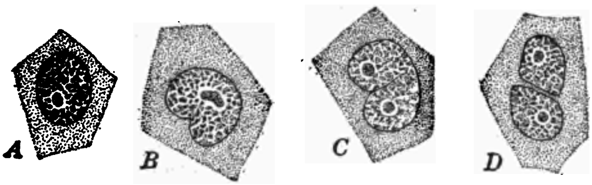


FIG. 7. Amitotic nuclear division in the follicle cells of a cricket's egg. (From Dahlgren and Kepner.)

The amitotic process is usually a sign of *senescence* or *decadence* in a cell. Many cells divide by mitosis so long as there is actual division of the cytoplasm as well as of the nucleus, but if the cell body fails to divide, the nucleus alone may continue to multiply amitotically, producing a multinucleate cell. "The commonly received idea, at present, concerning amitosis is that it is a terminal process in the cell's life activities, and is a method of securing more nuclear surface for use in forced metabolism or secretion" (21, p. 39).

In concluding this account of cell division two points are worthy of special emphasis. First, with regard to the *continuity of the chromatin*, it may be said that the chromatin is continuous from one cell generation to another. The cells resulting from mitosis may differ greatly in size, but the chromatin seems to be divided equally between them with great exactness. Second, *cells are never known to arise except from preexisting cells.* These two facts are perhaps the most important for us to keep in mind as we go on to study the more complex problems of fertilization and cell division in the many-celled animals, for growth in every Metazoon is really nothing more than cell division and cell growth.

3. The Cell Theory

Owing to the important place that cells have occupied in the development of our fundamental biological ideas, it seems proper to consider briefly the origin and growth of the cell theory. Cells were first described by Hooke, an Englishman, in 1665. He published a figure showing the minute structure of cork (Fig. 8).

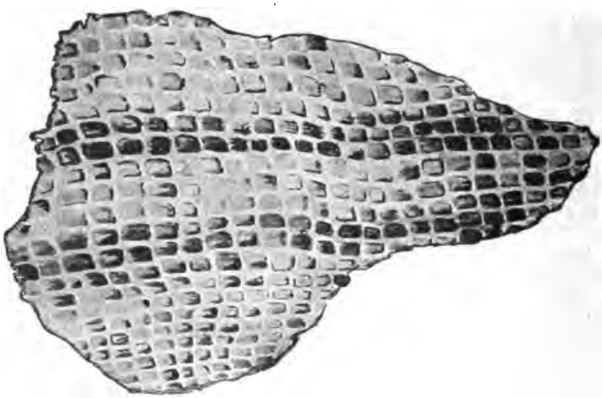


Fig. 8. Facsimile of a figure by Hooke representing cells of cork. (From Farmer in Lankester's Zoology.)

The regular arrangement of the compartments in this tissue reminded him of the cells of the monks in a monastery. For this reason they were given the name "cell," which they bear to this day. Several later investigators observed cellular structures in the tissues of plants and animals without realizing their importance.

In 1833, Brown, an English botanist, described the nucleus as a constant element of the cell. It was not, however, until the time of Schleiden, a botanist, and Schwann, a zoologist, that the cell theory was established. Schleiden, in 1838, published a small pamphlet in which he advanced the idea that all plants are composed of cells. A year later his colleague, Schwann, brought forth a more pretentious work in which he made the same generali-

zation concerning animals. It was largely due to the careful work of the latter that the cell theory was widely accepted throughout the scientific world.

The cell theory gave a basis for a comparison between plants and animals, as well as a new point of view in the study of the tissues of multicellular organisms. A host of investigators have entered the fields of histology and cytology; in fact, these are still the favorite subjects for anatomists.

The early investigators believed the cell wall to be the important part of the cell. Cohn, in 1847, observed that the protoplasm of certain lower plants left the wall at certain times and swam about in the water. This discovery initiated the idea that the wall is of minor importance as compared with the substance contained within it. It was later ascertained that many cells have no walls at all.

Perhaps the foremost of recent workers was Max Schultze, who recognized the cytoplasm and nucleus as the principal constituents of all cells, and, in 1861, defined a cell as *a mass of protoplasm containing a nucleus.* He also stated that both the nucleus and cytoplasm arise through the division of the corresponding elements of a preexisting cell. At the present time, though we retain the old designation "cell" for the units of protoplasm, it must be constantly borne in mind that the name refers to the living substance rather than to the wall, which may or may not be present.

A more fitting close for this chapter cannot be found than the words of Professor E. B. Wilson, the foremost American investigator of cellular phenomena.

"During the half century that has elapsed since the enunciation of the cell-theory by Schleiden and Schwann, in 1838–1839, it has become ever more clearly apparent that the key to all ultimate biological problems must, in the last analysis, be sought in the cell. It was the cell-theory that first brought the structure of plants and animals under one point of view, by revealing their common plan of organization. It was through the cell-theory

that Kölliker, Remak, Nägeli, and Hofmeister opened the way to an understanding of the nature of embryological development, and the law of genetic continuity lying at the basis of inheritance. It was the cell-theory again which, in the hands of Goodsir, Virchow, and Max Schultze, inaugurated a new era in the history of physiology and pathology, by showing that all the various functions of the body, in health and in disease, are but the outward expressions of cell activities. And at a still later day it was through the cell-theory that Hertwig, Fol, Van Beneden, and Strasburger solved the long-standing riddle of the fertilization of the egg and the mechanism of hereditary transmission. No other biological generalization, save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view, or has accomplished more for the unification of knowledge. The cell-theory must therefore be placed beside the evolution-theory as one of the foundation stones of modern biology" (25, p. 1).

CHAPTER IV

AMEBA

(*Ameba proteus* Leidy)

Ameba proteus (Fig. 9) is a one-celled animal about .25 mm. ($\frac{1}{100}$ inch) in diameter, and is, therefore, invisible to the naked eye. Under the compound microscope it appears as an irregular color-

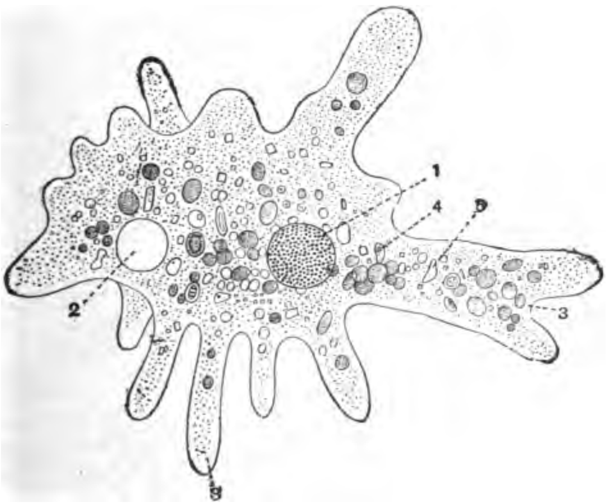


FIG. 9. *Ameba proteus.* *1*, nucleus; *2*, contractile vacuole; *3*, pseudopodia, dotted line leads to ectoplasm; *4*, food vacuoles; *5*, grains of sand. (From Shipley and MacBride after Gruber.)

less particle of animated jelly which is constantly changing its shape by thrusting out finger-like processes (Fig. 9, *3*).

Habitat and Collecting. — *Ameba proteus* lives in fresh-water ponds and streams. It may be obtained for laboratory use from a variety of places, such as the organic ooze from decaying vegetation or the lower surface of lily pads. Perhaps the most certain method is that suggested by Professor Jennings (37). About two weeks before the specimens are needed, a mass of pond weed (*Ceratophyllum* is the best) should be gathered, placed in flat dishes, and immersed in water. The vegetation soon decays, and a brown scum appears on the surface. In this scum Amebas may be found.

General Anatomy. — Two regions are distinguishable in the body of *Ameba*, an outer colorless layer of clear cytoplasm, the *ectosarc*, and a comparatively large central mass of granular cytoplasm, the *endosarc*. A single clear spherical body, usually lying near the end of the animal away from the direction of motion, and disappearing at more or less regular intervals, is the *contractile* or *pulsating vacuole* (Fig. 9, *2*). Suspended in the endosarc is a *nucleus* (Fig. 9, *1*), usually one or more *food vacuoles* (Fig. 9, *4*), material ready for excretion, foreign substances such as grains of sand (Fig. 9, *5*), and undigested particles, the amount of the latter depending upon the feeding activity of the specimen at the time when examined.

From this description it will be noted that *Ameba proteus* contains all of the essential constituents of a cell. It is, moreover, simple in structure, shows a number of physiological activities in their simplest form, is one of the most primitive of all animals, and is easily obtained. For these reasons it has been, and still is, a favorite subject for study.

Detailed Anatomy. — The *ectoplasm* (Fig. 9, *3*) is easily distinguished from the endoplasm because of the absence within it of granules. The ectoplasm is firmer than the endoplasm, probably because the outer protoplasm tends to stiffen under the influence of surface tension.

The *endoplasm* occupies the central portion of the body. Being less dense than the ectoplasm, it contains within it all of the

large granules. No fixed line of separation between it and the ectoplasm is possible.

The *nucleus* (Fig. 9, *1*) is not easily seen in living specimens. In animals that have been properly killed and stained it appears as a spherical body lying in the endoplasm. Its position is not definite, but changes during the movements of the *Ameba*. It has a firm membrane and contains a great many spherical particles of chromatin scattered about in the nuclear sap. During the life of *Ameba*, before the period of reproduction, the nucleus plays an important rôle in the metabolic activity of the cell. This has been proved by experiments in which the animal was cut in two. Invariably the vital processes were disturbed in the enucleated fragment, and death resulted. Profound changes in the nucleus take place during reproduction; these will be described in detail later.

The *contractile vacuole* (Fig. 9, *2*) is a clear space filled with a fluid less dense than the surrounding protoplasm. It derives its name from the fact that at more or less regular intervals it suddenly disappears, its walls having contracted, thus forcing out the contents. That the vacuole discharges to the outside of the body has not been definitely observed in *Ameba*, no doubt because the fluid is usually expelled on the upper surface of the body and therefore cannot be seen (38). "At first the vacuole lies near the nucleus, but as it grows, it becomes separated from the latter, and at the time of its contraction lies at the end of the body farthest from the advancing pseudopodia, at what is sometimes called the posterior end. Its reappearance is always somewhere near its point of disappearance. While still small it is carried along by the streaming protoplasm back to a position near the nucleus, where it completes its development" (29, p. 88, Fig. 10).

The functions of the contractile vacuole are excretory and respiratory, as is explained on page 50. Several investigators have recently regarded it as a hydrostatic organ, regulating the quantity of water contained in the body of the animal, and so its weight. This would also afford a means of getting rid of the water taken

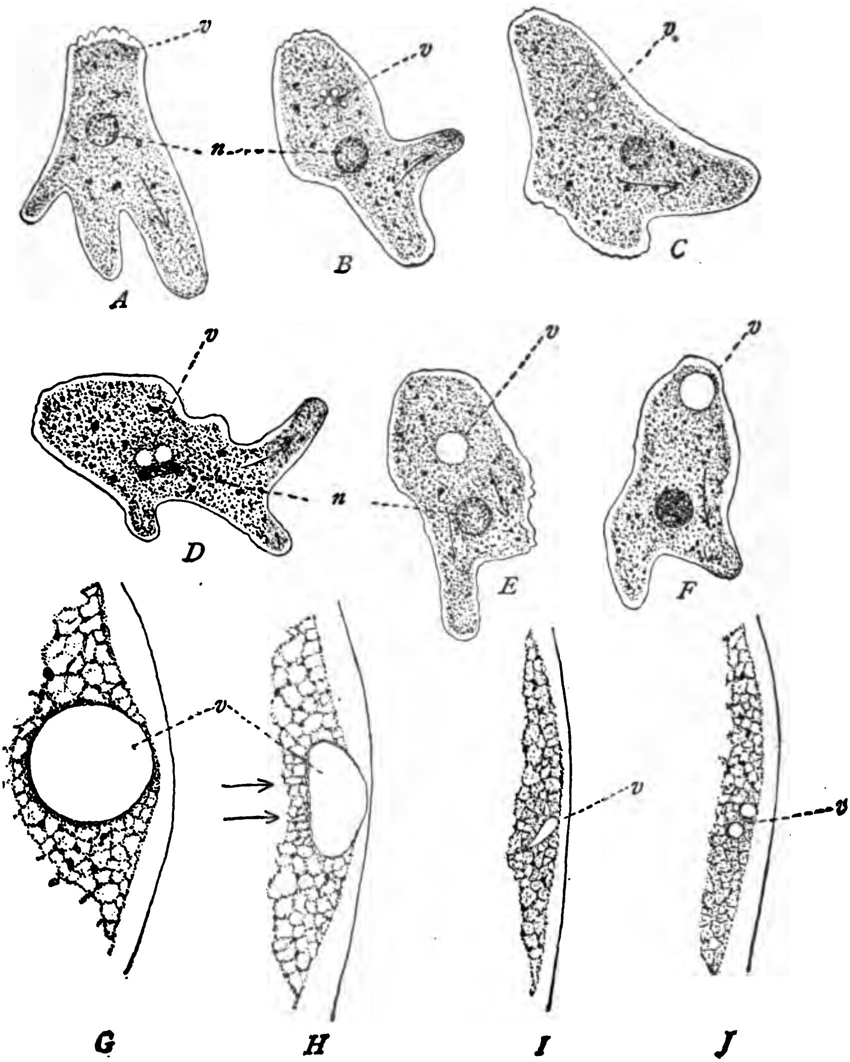


FIG. 10. *Ameba proteus.* A, B, C, D, E, F, show successive stages in the growth of the contractile vacuole (*v*); G, H, I, and J, show four stages in the contraction of the vacuole. (From Calkins.)

in by the protoplasm through the body wall and consequently regulating the tension between the protoplasm and the surrounding water. Death by diffluence is thus prevented.

Food vacuoles (Fig. 9, *4*) are produced when food is taken into the body. Such a vacuole has as its nucleus a particle of nutritive material and is a sort of temporary stomach.

Locomotion. — Although extremely simple in structure, *Ameba* carries on practically all of the vital activities characteristic of the higher animals. It is capable of automatic movement, of reacting to various stimuli, of carrying on metabolic processes, of growth, and of reproduction. These are all fundamental properties of protoplasm (Chap. II, p. 10) and are here exhibited in their simplest form.

The *locomotive function* is located in the ectoplasm. The motile organs are finger-like protrusions of cytoplasm called *pseudopodia.* A pseudopodium is formed in the following manner. The ectoplasm bulges out and enlarges until a blunt projection is produced; the endoplasm then flows into it. The result is a movement of the entire animal in the direction of the pseudopodium. If more than one is formed at the same time, there occurs a struggle for supremacy until finally one survives while the others flow back and gradually disappear. *Ameba* moves, therefore, by thrusting out pseudopodia and then flowing into them. It is necessary to distinguish between pseudopodia that adhere to the surface of some object and those that are thrust out freely into the surrounding fluid, since an hypothesis that explains the formation of one does not always account for the other.

There are three principal theories which attempt to explain the formation of pseudopodia; these may be outlined briefly as follows: —

(1) **The Adherence Theory.** — It was long ago discovered that if a drop of inorganic fluid which is spreading on a solid surface is made to adhere on one side more strongly than the other, it will move toward the former side. This fact suggested that the

body of the *Ameba* may move in a certain direction for the same reason (27). This theory, however, accounts only for the pseudopodia that are attached, and does not explain free pseudopodia.

(2) **The Surface Tension Theory.** — According to the surface tension theory, local changes in the surface tension produce currents which move forward in the central axis and backward along the surface (28, 44). It has been shown, however, that the currents do not run in this manner (34).

(3) **The Contractile Theory.** — Many early investigators held the view that the contractility of the protoplasm accounts for changes which take place in a moving *Ameba.* This theory was later given up by most zoologists because the currents in the protoplasm began at the point of advance and extended backward

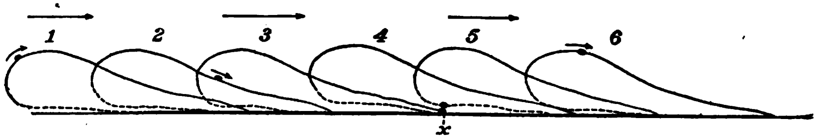


FIG. 11. Diagram of the movements of a particle attached to the outer surface of *Ameba verrucosa,* in side view. (From Jennings.)

instead of commencing at the hinder end or in the center. Two recent authors have again brought forth evidence which tends to show that after all the contraction theory is the correct interpretation. Jennings (39) by mixing soot in water was able to show that *Ameba verrucosa* resembles an elastic sac filled with a fluid. Specimens were placed in water containing some fine soot. The particles became attached to the surface of the animal and the currents in the ectoplasm could easily be determined by watching their movements. From these observations the following conclusions were reached. "In an advancing Amœba substance flows forward on the upper surface, rolls over at the anterior edge, coming in contact with the substratum, then remains quiet until the body of the Amœba has passed over it. It then

moves upward at the posterior end, and forward again on the upper surface, continuing in rotation as long as the Amœba continues to progress. The motion of the upper surface is congruent with that of the endosarc, the two forming a single stream" (39, p. 148, Fig. 11). "The movement can be imitated roughly by making a cylinder of cloth, laying it flat on a plane surface, and pulling forward the anterior edge in a series of waves. The entire cylinder then rolls forward just as the Amœba does" (39, p. 145). Jennings's observations have been confirmed for *Ameba verrucosa*, but do not seem to explain the phenomena in moving specimens of *Ameba proteus* and other species (34).

A new method of making observations has enabled Dellinger (34) to add materially to our knowledge of the movements of

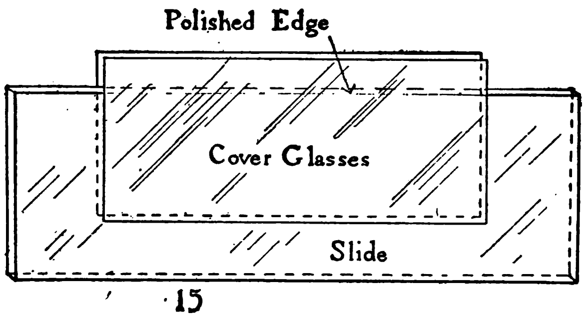


FIG. 12. Diagram of apparatus designed to study *Ameba* in side view. (From Dellinger in *Journ. Exp. Zool.*)

Ameba proteus. This investigator examined specimens from the side by means of the following apparatus (Fig. 12): One edge of a slide was ground square and polished. Long cover slips were cemented to this with the edges extending beyond the polished surface so as to form a narrow trough. With the microscope brought to a horizontal position, specimens pipetted into the trough could be observed in side view as they moved along the edge of the slide. Observations made in this way seemed to prove that *Ameba* moves by means of a contractile substance.

In advancing the *Amebæ* "extend the anterior end free in the water and attach it at or near the tip and then contract. At the

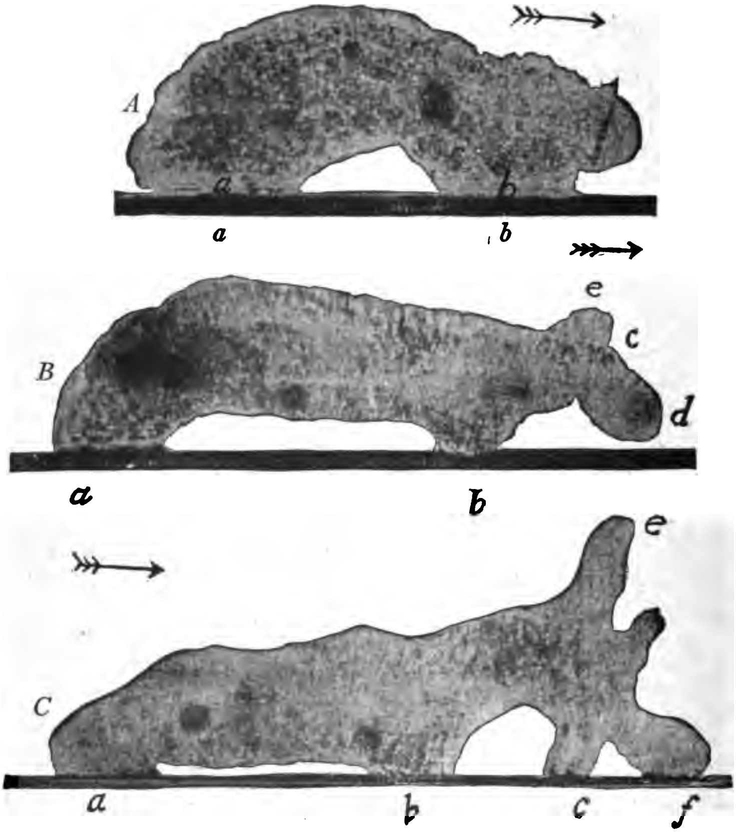


FIG. 13. Photographs of *Ameba proteus* in side view to show method of locomotion. A, B, and C show a specimen attached at two points *a* and *b*; the pseudopod projecting from one end bends down to the substratum as shown in B at *d*; C shows two more attached pseudopods at *c* and *f*, and several free pseudopods at *e*.

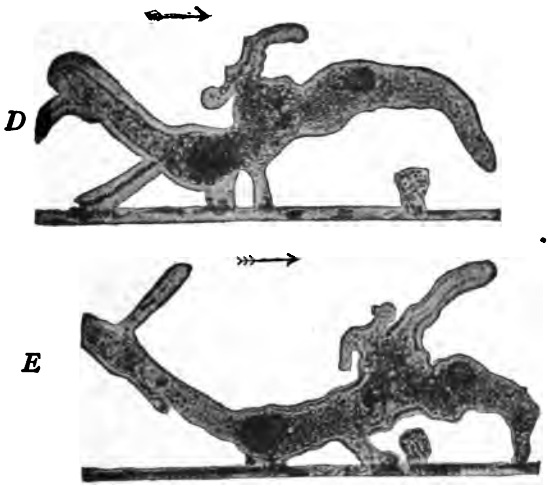


FIG. 13 — *continued.* D and E show the extension and attachment of a long thin pseudopod. (From Dellinger in *Journ. Exp. Zool.*)

same time the posterior end is contracting and the substance thus pushed and pulled forward goes to form the new anterior end. This continues as long as the *Ameba* advances (Fig. 13, A, B, C). Often the anterior end is pushed along the substratum, but no attachments form except at definite points.

"In other cases the anterior end is lifted free and then curves down to the substratum and attaches, forming a long loop. The posterior end is then released, and the substance flows over to the anterior end. At the same time another anterior end is extended" (34, p. 351, Fig. 13, D, E). When creeping on the ceiling the movements are the same as when creeping on the floor. When beginning to move, pseudopodia are extended in all directions until one becomes attached, when the animal advances in the direction of the point of attachment. That a contractile substance is present in *Ameba* and accounts for its movements seems to be proven by Dellinger's observations.

Many attempts have been made to *imitate the movements of*

Ameba by means of inorganic substances, in an endeavor to discover the physical or chemical nature of its locomotion (40). Even when an apparently reliable imitation is produced, we cannot be certain that the forces at work are actually those which cause the movements of *Ameba*. Practically all of the imitations thus far reported depend on surface tension.

One method of producing ameboid movements is as follows (26). A large drop of mercury is placed in a flat-bottomed watch glass and covered with 10 per cent nitric acid. A piece of potassium bichromate when placed near the mercury produces a solution which causes local lowering of the surface tension of the drop, and results in the formation of projections and movement of the mercury in various directions.

Metabolism. — The various metabolic activities of animals were discussed in Chapter II, pages 13 to 15. In *Ameba* these processes are seen in their simplest form, and will, therefore, be considered in some detail in spite of the danger of repetition. The entire series of processes connected with the manufacture and destruction of protoplasm are the ingestion of food, digestion, egestion, absorption, circulation, assimilation, dissimilation, secretion, excretion, and respiration.

Food. — The food of *Ameba* consists of very small aquatic plants such as *Oscillaria*, and diatoms, Protozoa, bacteria, and other animal and vegetable matter. A certain amount of choice of food is exercised, or its body would become overloaded with particles of sand and other indigestible material among which it lives. Furthermore, it seems to evince a preference for diatoms which one would think too large for easy consumption. This apparent choice of food may be due to ordinary physical laws of fluids.

Ingestion. — The ingestion, or taking in of food, occurs without the aid of a mouth. Food may be engulfed at any point on the surface of the body, but it is usually taken in at what may be called the temporary anterior end, that is, the part of the body toward the direction of locomotion. Jennings describes inges-

tion as follows. The *Ameba* flows against the food particle, which does not adhere but tends to be pushed forward away from the animal (Fig. 14, *1*). That part of the body directly back of the food ceases its forward movements while, on either side and above, pseudopodia are extended which gradually form a concavity in which the food lies (Fig. 14, *2*) and finally bend around the particle (Fig. 14, *3*) until their ends meet and fuse

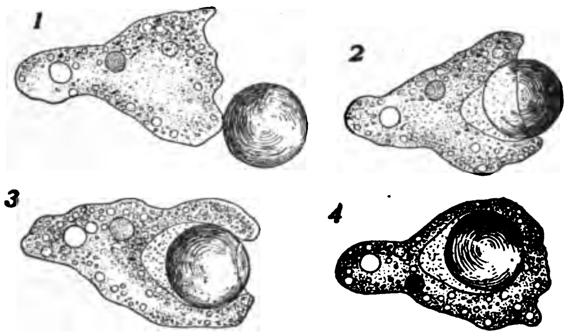


FIG. 14. *Ameba* ingesting a *Euglena* cyst. 1, 2, 3, 4, successive stages in the process. (From Jennings.)

(Fig. 14, *4*). A small amount of water is taken in with the food, so that there is formed a vacuole whose sides were formerly the outside of the body, and whose contents consist of a particle of nutritive material suspended in water. The whole process of food-taking occupies one or more minutes, depending on the character of the food. *Ameba* is not always successful in accomplishing what it undertakes, but when it does not capture its prey at once, it seems to show a persistence usually only attributed to higher organisms. No doubt the reactions in food-taking depend upon both mechanical and chemical stimuli (39).

Imitations of the engulfing of food by *Ameba* have been devised, based on the theory that ingestion depends on the physical adhesion between the liquid protoplasm and the solid food. Drops of water, glycerin, white of egg, etc., will draw into con-

tact and engulf solid particles of various kinds. One of the most ingenious of these imitations is that reported by Rhumbler of the ingestion of a filament of *Oscillaria* (44). A thread of shellac is brought into contact with a drop of chloroform in a watch glass of water. The drop adheres to the filament, lengthens along it, and, because of its tendency to again become spherical, succeeds in bending the now softened thread. The tension of the surface film gradually draws in more of the filament, until finally

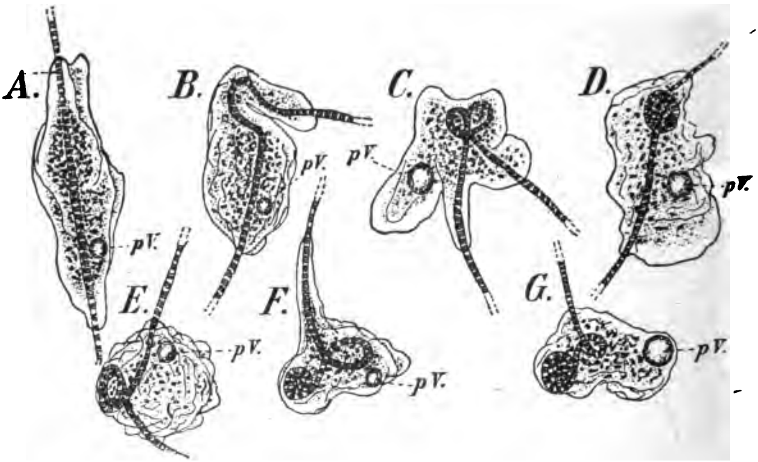


FIG. 15. *Ameba verrucosa* devouring a filament of *Oscillaria*. (From Rhumbler in Archiv f. Entwick.-mech.)

the whole thread is embedded in a complicated coil within the drop. The ingestion of *Oscillaria* by *Ameba* is quite similar (Fig. 15).

Choice of food may also be imitated with inorganic substances. For example, a drop of chloroform in a watch glass of water will take in shellac, paraffin and other substances, and will reject sand, wood, glass, etc. (40). The substances accepted are those which adhere to the drop of chloroform. Since in the majority of cases food particles do not stick to the surface of the

Ameba, we cannot explain ingestion by means of these physical imitations.

Digestion. — Digestion takes place without the aid of a stomach. After a food vacuole has become embedded in the endoplasm its walls pour into it a secretion of some mineral acid, probably HCl. "It is probable that the minute particles of nucleoproteids that are constantly arising in the neighborhood of the nucleus contain certain digestive ferments which stimulate the formation of the mineral acid in the vicinity of the gastric vacuole" (32, p. 79). The digestive fluid seems to dissolve only proteid substances, having no effect upon fats and carbohydrates. That the nucleus plays an important rôle in digestive processes was shown by Hofer (36), who found that if a well-fed *Ameba* was cut in two, the non-nucleated portion was unable to digest food.

Egestion. — Indigestible particles are egested at any point on the surface of the *Ameba*, there being no special opening to the exterior for this waste matter. Usually such particles are heavier than the protoplasm, and as the animal moves forward they lag behind, finally passing out at the end away from the direction of movement; that is, *Ameba* flows away, leaving the indigestible solids behind.

Assimilation. — The peptones, derived from the digestion of proteid substances, together with the water and mineral matter taken in when the gastric vacuole was formed, are absorbed by the surrounding protoplasm and pass into the body substance of the animal, no circulatory system being present so far as we know. These particles of organic and inorganic matter are then assimilated; that is, they are rearranged to form new particles of living protoplasm, which are deposited among the previously existing particles. The ability to thus manufacture protoplasm from unorganized matter, it will be remembered, is one of the fundamental proper ties of living substance (p. 10).

Dissimilation. — The energy for the work done by *Ameba* comes from the breaking down of complex molecules by oxidation or "physiological burning." This is known as dissimilation or

katabolism. The products of this slow combustion are the energy of movement, heat, and residual matter. Ordinarily this consists of solids and fluids, mainly water, some mineral substances, urea and CO_2. Secretions, excretions, and the products of respiration are included in this list.

Secretion. — We have already noted that an acid is poured into the gastric vacuole by the surrounding protoplasm. Such a product of dissimilation, which is of use in the economy of the animal, is known as a secretion.

Excretion. — Materials representing the final reduction of substances in the process of katabolism are called excretions. These are deposited either within or outside of the body. A large part of the excretory matter, including urea and CO_2, passes through the general surface of the body. The fluid content of the contractile vacuole is known to contain urea, therefore this organ is excretory in function. It is also *respiratory*, since CO_2 probably makes its way to the exterior by way of this organ. Oxygen dissolved in water is taken in through the surface of the body. This gas is necessary for the life of the animal; if replaced by hydrogen, movements cease after twenty-four hours; if air is then introduced, movements begin again; if not, death ensues (42).

Growth. — If food is plentiful, more substance is added to the living protoplasm of the *Ameba* than is used up in its various physical activities. The result is an increase in the volume of the animal. This is growth, and, as in all other living organisms, growth by the addition of new particles among the preëxisting particles, *i.e.* growth by *intussusception.*

Reproduction. — There is, however, a limit with regard to the size that may be attained by *Ameba proteus*, as it rarely exceeds .25 mm. ($\frac{1}{100}$ inch) in diameter. When this limit is reached, the animal divides into two parts. Why should there be such a limit? The following explanation is given by Herbert Spencer and others. The volume of an organism varies as the cube of its diameter, the surface as the square. Thus, as an animal grows, the ratio between surface and volume decreases; and, since

Ameba takes in food, gives off waste material, and carries on respiration through its surface, the activities of the cell must decrease with increase in size until further growth is impossible. The solution of the problem is the division of the animal into two, whereby the original ratio between surface and volume is restored. Reproduction by binary division, therefore, takes

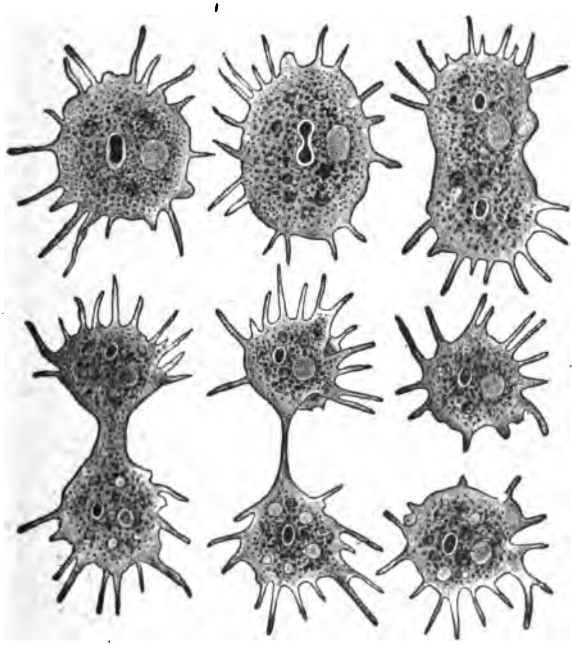


FIG. 16. *Ameba polypodia* dividing by binary fission. (From Parker and Haswell after F. E. Schulze.)

place when growth is no longer possible. It is supposed that this division is inaugurated through some unknown change in the relations between the nucleus and cytoplasm. There are at least two kinds of reproduction in *Ameba proteus*, but neither has ever been satisfactorily worked out in detail. They are (1) binary division and (2) sporulation.

(1) During *binary division* the nucleus apparently divides amitotically, although indications of mitosis have been reported. A definite mitotic figure is formed in certain species of *Ameba, e.g. Ameba binucleata* (Fig. 17). While the nucleus is elongating, a constriction appears around the middle of the cell; the nucleus then separates into two apparently equal parts which move toward the ends of the animal. Meanwhile the constriction of the body has grown deeper, and finally severs the connection between the two ends, and two daughter Amebæ result (47, Fig. 16).

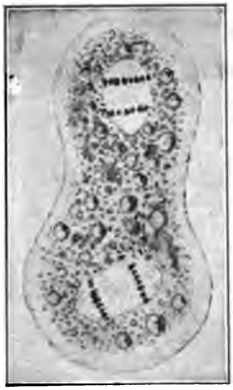


FIG. 17. *Ameba binucleata* beginning to divide. Both nuclei have formed mitotic figures. (From Lang after Schaudinn.)

(2) Scheel (46) seems to be the only person who has ever witnessed *sporulation* in *Ameba proteus*. The whole process lasted from two and one half to three months. The pseudopodia were first drawn in and the animal became spherical. A three-layered cyst was then secreted. The *Ameba* rotated within this for several days, after which all movements ceased. The nucleus divided until there were twenty or thirty present, arranged near the surface. Continued division resulted in an increase of nuclei to from five hundred to six hundred. The central part of the body had none. Cell walls now appeared at the periphery, cutting off the nuclei, each with a small amount of the surrounding cytoplasm. The wall of the cyst became soft, broke, and allowed the small Amebæ to escape. Hundreds of these *Amebulae*, or *pseudopodiospores*, as they are sometimes called, broke out at one time. They became recognizable as *Ameba proteus* in from two and a half to three weeks. No reason could be discovered for sporulation, although experiments were conducted in which specimens were starved, were given an excess

of food, were allowed to desiccate, and were transferred to water from different localities; none of these resulted in encystment and sporulation.

The development of *Ameba* is simply a matter of growth; both the spores and the daughter cells resulting from binary division become full-grown specimens by means of a gradual increase in volume.

Behavior of Ameba. — The sum total of all the various movements of an animal constitute what is known as its behavior. In *Ameba* these movements may be separated into those connected with locomotion and those resulting from external stimuli. We have already given an account of the locomotion of *Ameba*, and so shall confine ourselves now to a discussion of its responses to different kinds of stimuli. The reactions of *Ameba* to stimuli have been grouped by Jennings (39, 41) into positive, negative, and food-taking. The last named were discussed on page 47. The following account, then, will deal with positive and negative reactions of *Ameba proteus* to external stimulation.

Definitions of Terms. — First, it will be well to define a few of the terms used in describing the motor responses of animals to stimuli. A reaction resulting from a change in an animal's environment, *e.g.* an increase in the intensity of the light, is known as " tropism " or " taxis." The term " tropism " means " to turn "; it is used instead of saying that an animal " likes " or " dislikes " certain stimuli, because we can determine by experiment which way an individual will turn under various conditions, but are not in a position to decide whether " likes " or " dislikes " enter into the phenomena. The kind of stimulus employed is indicated by a prefix. The principal kinds of tropisms are as follows: —

(1) Thigmotropism = reaction to contact.
(2) Chemotropism = reaction to a chemical.
(3) Thermotropism = reaction to heat.
(4) Phototropism = reaction to light.
(5) Electrotropism = reaction to electric current.

(6) Geotropism = reaction to gravity.
(7) Chromotropism = reaction to color.
(8) Rheotropism = reaction to current.

"Taxis" is often employed instead of "tropism" when the terms read "thigmotaxis," "chemotaxis," etc. If the animal reacts by a movement toward the stimulus, such as light, it is said to be positively phototropic, phototactic, etc.; if away from the stimulus, negatively phototropic or phototactic, etc. *Ameba* has been found to respond to contact with solids, to chemicals, to heat, to light, to colors, and to electricity. After describing the reactions of *Ameba* to each of the above-named stimuli, the general significance of its behavior will be considered.

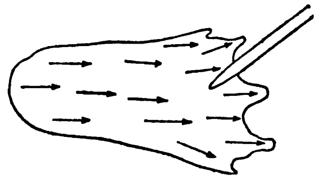


FIG. 18. *Ameba* stimulated by glass rod.

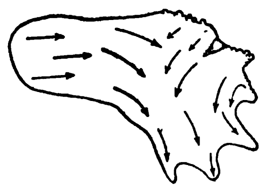


FIG. 19. *Ameba* moves always from mechanical stimulus. (From Jennings.)

Thigmotropism. — If a moving *Ameba* is touched at any point with a solid object, *e.g.* a glass rod, the part affected contracts and moves away. If the anterior edge is stimulated in this way, the part touched stops and contracts while a new pseudopodium is pushed out in some other place and the animal moves away in another direction (Fig. 19). This is clearly a negative reaction, and the animal is said to be negatively thigmotropic. There are, however, certain conditions which call forth positive responses to contact with solids. For example, if the *Ameba* is floating freely in the water and a pseudopodium comes in contact with the substratum (Fig. 20) the animal moves in the direction of the pseudopodium stimulated until the normal creeping position has been attained. Contact with food also results in positive reactions, as described on pages 47 and 48. *Ameba*, there-

fore, reacts negatively to a strong mechanical stimulus and positively to a weak one.

Chemotropism. — *Ameba* is sensitive to changes in the chemical composition of the water surrounding it. If a chemical is

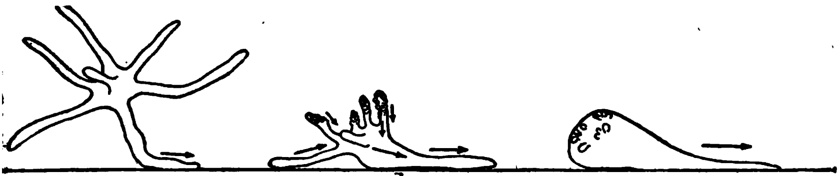
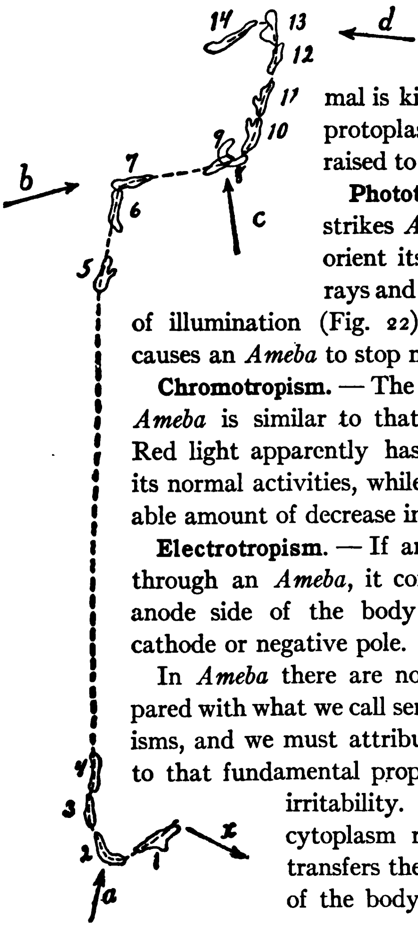


FIG. 20. Method by which a floating *Ameba* passes to a solid. (From Jennings.)

brought into contact with one side by means of a fine capillary glass rod or tube, the part affected contracts and the animal moves off in some other direction (Fig. 21). "It has been shown to react negatively when the following substances come in contact with one side of its body: methylene blue, methyl green, sodium chloride, sodium carbonate, potassium nitrate, potassium hydroxide, acetic acid, hydrochloric acid, cane sugar, distilled water, tap water, and water from other cultures than that in which the *Amœba* under experimentation lives" (41, p. 10).

FIG. 21. Negative reaction to chemical stimulation in *Ameba*. A little methyl green diffuses against the advancing end, causing new pseudopodia to be thrust out, and a change in the direction of movement. (From Jennings.)

Thermotropism. — *Ameba* gives a negative response if locally affected by heat. This may be accomplished by bringing a heated needle in front of an *Ameba* which is creeping along on the under surface of a cover glass. When this is done, the animal moves off in another direction. The degree of temperature also has an influence upon the rate of the normal movements. Cold and excessive heat retard its activities, while a moderate amount of heat increases the move-



ment. Activity ceases altogether between 30° and 35° C., and the animal is killed by coagulation of the protoplasm if the temperature is raised to 40° C.

Phototropism. — If a strong light strikes *Ameba* from the side, it will orient itself in the direction of the rays and move away from the source of illumination (Fig. 22). Ordinary white light causes an *Ameba* to stop moving (35).

Chromotropism. — The effect of blue light upon *Ameba* is similar to that of ordinary white light. Red light apparently has no effect whatever upon its normal activities, while other colors cause a variable amount of decrease in its movement.

Electrotropism. — If an electric current is passed through an *Ameba*, it contracts on the positive or anode side of the body and moves toward the cathode or negative pole.

In *Ameba* there are no organs that can be compared with what we call sense organs in higher organisms, and we must attribute its reactions to stimuli to that fundamental property of protoplasm called irritability. The superficial layer of cytoplasm receives the stimulus and transfers the effects to some other part of the body; thus may be shown the phenomenon of internal irritability or conductivity. Perhaps the most primitive method in the animal kingdom of a reaction to stimuli is illus-

FIG. 22. Reaction of *Ameba* to light. The arrows indicate the direction of the light rays and the numbers the successive positions assumed by the animal. The *Ameba* always moves away from the source of light. (From Jennings after Davenport.)

trated by the response of a definite point on the body of *Ameba* to a strong mechanical stimulus. This may be compared with what happens when a mass of inorganic material is acted upon by a force; here a reaction is produced directly at the point of contact. In orienting itself in the direction of the light rays, *Ameba* shows a response to a continuous stimulus which affects the entire body (Fig. 22); if the source of illumination is changed, the animal changes its orientation. The cause of the reaction, as in the above instance, seems to be in most cases a change in the environment. The response is always produced by a stimulation directly preceding it, but the animal soon becomes acclimated to the new environment, and its activities become normal. This is shown when it is transferred from one culture to another (chemotropism) or when white light is thrown upon it (phototropism).

The reactions of *Ameba* to stimuli are of undoubted value to the individual and to the preservation of the race, for in every instance the negative reaction is produced by injurious agents such as strong chemicals, heat, and mechanical impacts, while positive reactions are produced by beneficial agents. The responses, therefore, in the former cases carry the animal out of danger, in the latter, toward a safer haven.

Ameba is of fundamental interest to animal psychologists, since it represents the "animal mind" in its most primitive form. The behavior of *Ameba* in the absence of external stimuli, for example when it is suspended freely in the water, shows that some of its activities are initiated by internal causes. Whether or not the animal is in any degree conscious is a question still unanswered. If *Ameba* has recognizable sensations, they must be infinitely less in both quality and quantity than in higher organisms. Furthermore, it is unable to learn from the few kinds of experiences it does pass through, and is therefore lacking in memory images. One case in which an *Ameba* attempted to capture another is recorded by Jennings, and seems to point to something higher than mere physical and chemical attractions.

In this instance a large animal showed decided persistence in its endeavors to engulf a smaller *Ameba;* several times it reversed its course and continued the pursuit.

A review of the facts thus far obtained seems to show that factors are present in the behavior of *Ameba* "comparable to the habits, reflexes, and automatic activities of higher organisms" (39, p. 234), and "if Amœba were a large animal, so as to come within the everyday experience of human beings, its behavior would at once call forth the attribution to it of states of pleasure and pain, of hunger, desire, and the like, on precisely the same basis as we attribute these things to the dog" (41, p. 336).

CHAPTER V

PARAMECIUM

(*Paramecium caudatum* Ehrbg.)

Paramecium, like *Ameba,* is a unicellular organism, but is further advanced in the scale of life. It also is found in fresh water ponds and streams, and is very easily obtained. Cultures prepared for *Ameba* will in most cases sooner or later contain a host of *Paramecia.*

General Anatomy. — If a drop of water containing *Paramecia* is placed on a slide, the animals may be seen with the naked eye moving rapidly from place to place. Under the microscope they appear cigar-shaped (Fig. 23). A closer view reveals a depression (*o.g.*) extending from the end directed forward in swimming, obliquely backward and toward the right, ending just posterior to the middle of the animal. This is the so-called *oral groove* or *peristome.* The *mouth* (*m.*) is situated near the end of the oral groove. It opens into a funnel-shaped depression called the *cytopharynx* or *gullet* (*g.*), which passes obliquely downward and posteriorly into the *endosarc* (*en.*). The oral groove gives the animal an unsymmetrical appearance. Since *Paramecium* swims with the slender but blunt end foremost, we are able to distinguish this as the *anterior end.* The opposite end, which is thicker but more pointed, represents the *posterior end,* while the side containing the oral groove may be designated as *oral* or *ventral,* the opposite side *aboral* or *dorsal.* The motile organs are fine threadlike *cilia* regularly arranged over the surface. Two layers of cytoplasm are visible, as in *Ameba,* an outer comparatively thin clear area, the *ectosarc* (*ec.*) and a central granular mass, the *endosarc* (*en.*). Besides these a distinct *pellicle* (*p.*) or *cuticle* is present

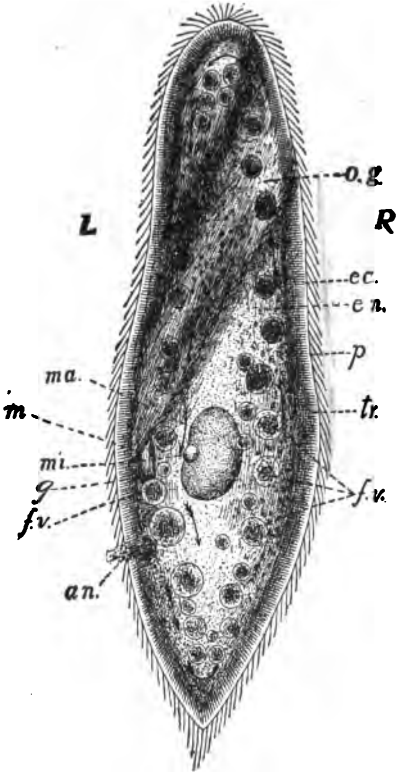


FIG. 23. *Paramecium* viewed from the oral surface. L, left side; R, right side. *an.*, anus; *ec.*, ectosarc; *en.*, endosarc; *f.v.*, food vacuoles; *g.*, gullet; *m.*, mouth; *ma.*, macronucleus; *mi.*, micronucleus; *o.g.*, oral groove; *p.*, pellicle; *tr.*, trichocyst layer. The arrows show the direction of movement of the food vacuoles. (From Jennings.)

outside of the ectosarc. Lying in the ectoplasm are a great number of minute sacs, the *trichocysts* (*tr.*), which discharge long threads to the exterior when properly stimulated. One large *contractile vacuole* is situated near either end of the body, close to the dorsal surface, while a variable number of *food vacuoles* (*f.v.*) may usually be seen. The *nuclei* are two in number, a large *macronucleus* (*ma.*) and a smaller *micronucleus* (*mi.*); these are suspended in the ectoplasm near the mouth opening. The *anal spot* (*an.*) can be observed only when solid particles are discharged. It is situated just behind the posterior end of the oral groove.

Detailed Anatomy. — The *endoplasm* (Fig. 23, *en.*) of *Paramecium* occupies the central part of the body. It is supposed to be alveolar in structure. Most of the larger granules contained within it are shown by microchemical reactions to be reserve food particles; they flow from place to

place, indicating that the protoplasm is of a fluid nature. The *ectoplasm* (*ec.*) does not contain any of the large granules characteristic of the endoplasm, since its density prevents their entrance. In this respect the two kinds of cytoplasm resemble the ectoplasm and endoplasm of *Ameba.* Outside of the ectoplasm is a delicate elastic membrane, the *pellicle* (*p.*) or *cuticle.* If a drop or two of 35 per cent alcohol is added to a drop of water containing *Paramecia,* the pellicle will be raised in some specimens in the form of a blister. Under the higher powers of the microscope the pellicle is then seen to be made up of a great number of hexagonal areas produced by *striations* on the surface (Fig. 24, A). These striations are really very fine grooves (Fig. 24, B), which cross one another obliquely.

The distribution of the motile organs, the *cilia,* corresponds to the arrangement of the striations on the cuticle, since one cilium projects from the center of each hexagonal area (Fig. 24, A). These thread-like structures occur on all parts of the body, those at the posterior end being slightly longer than elsewhere (Fig. 23). A cilium may be compared to a very fine pseudopodium which has become a permanent structure. It is an outgrowth of the cell protoplasm, coming from a basal body called a microsome (Fig. 24, B, *B*) which appears to arise from the nucleus. The structure and movements of cilia have been studied by investigators for many years, and the following theories have been proposed to explain them: (1) Cilia are somewhat stiff, lifeless processes attached to the cell and moved by active elements within the cell body (49). (2) Cilia are hollow elastic sheaths into which a fluid is injected and withdrawn. (3) Cilia consist of a complex fluid owing its contractility "to the presence of a filament of kinetic granules, placed along one edge of the cilium, the contraction of this thread furnishing the power of the cilium" (52, p. 49). (4) Cilia are fibrillar, the movements being due to the contraction of the fibrils. We are inclined to favor the last theory, since the movements can only be adequately explained by the presence of a contractile framework. Fibrils have been

demonstrated in the *flagella* of several unicellular animals, a flagellum being a large cilium. For example, in a Protozoon *Euglena* (see p. 85), the flagellum consists of four fibrils which extend its entire length. These are twisted about one another in a spiral of two and one half turns. They can be traced into the animal, where they branch out into a system of rootlets (Fig. 25). In the smaller cilia these fibrils have not been seen,

FIG. 25. Structure of the flagellum of *Euglena*. (From Dellinger in *Journ. Morph.*)

but are probably present; at least, we can account for all the movements made by cilia if such a condition exists as in the flagellum of *Euglena*. A fusion of cilia frequently takes place, forming *membranelles*. In *Paramecium* this has occurred within the mouth cavity, producing the *undulating membrane* (Fig. 29, *Mb*). This is attached to the dorsal wall of the mouth, and guides the food particles that are swept within its reach.

Just beneath the cilia, embedded in the cortical layer of the ectoplasm, is a uniform layer of spindle-shaped structures $\frac{4}{1000}$ mm. in length, lying with their long axes perpendicular to the surface (Fig. 24, A, *tr.*, Fig. 24, B, *T*). These are *trichocysts*. Their distribution is shown in surface view in Figure 24, A. They appear to be cavities in the ectoplasm filled with a semi-liquid homogeneous substance which is very refractive. They arise in the neighborhood of the nucleus, and probably from it (72). A small amount of osmic or acetic acid, when added to a drop of water containing *Paramecia*, causes in some cases the discharge of the trichocysts to the exterior through very small canals. This explosion is due to the pressure derived from the contraction of the cortical layer of the ectoplasm. After the explosion,

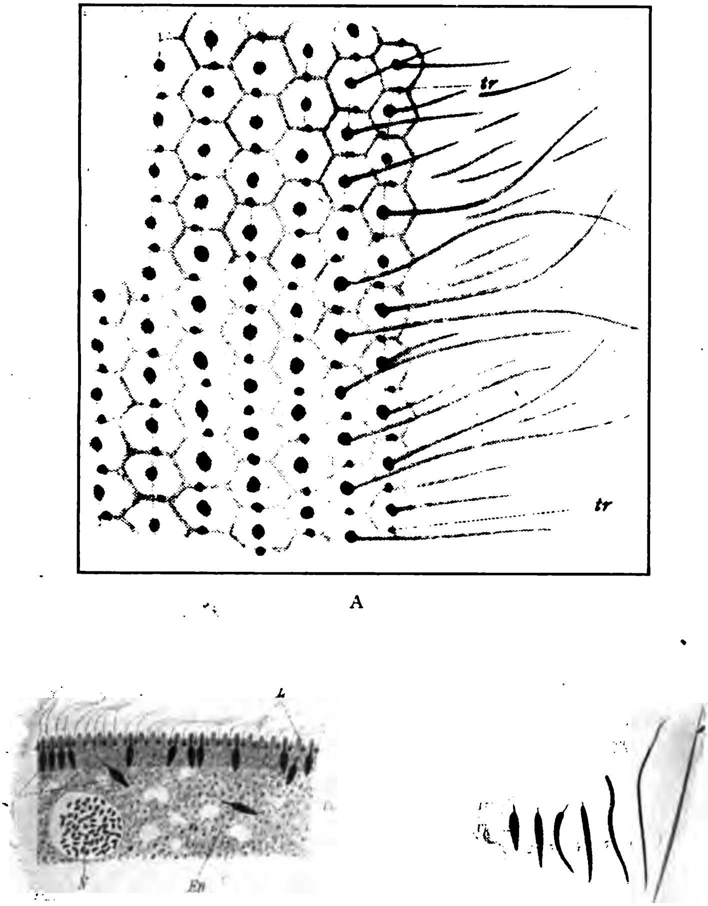


FIG. 24. Parts of *Paramecia* showing cilia and trichocysts. A, Surface view showing striations, cilia, and trichocysts (*tr.*); B, part of a cross section showing ridges (*L*) on the surface, cilia (*C*) coming from microsomes (*B*), trichocysts cut longitudinally (*T*) lying in the ectosarc (*Co*), and trichocysts (*T*) and a food vacuole (*N*) lying in the endoplasm (*En*). C, trichocysts in various stages of extrusion; ***Tk***, body of the structure; ***Tf***, the hairlike projection. (A from Schuberg; B, C from Maier in *Archiv f. Protist.*)

the trichocysts appear as long threads which have been extended to about eight times their former length (Fig. 24, C). Trichocysts are supposed to function as weapons of offense and defense. It is said that their contents are discharged with considerable force and that they contain a poison strong enough to paralyze any single-celled animal. The only evidence we have that the trichocysts are weapons of defense is furnished when *Paramecium* encounters its enemy *Didinium*. If the seizing organ of this Protozoon becomes fastened in the *Paramecium*, a great number of trichocysts near the place of the injury are discharged (Fig. 26). These produce a substance which becomes jelly-like on entering the water; this tends to force the two animals apart, and, if the *Paramecium* is a large one, frequently it succeeds in making its escape (70).

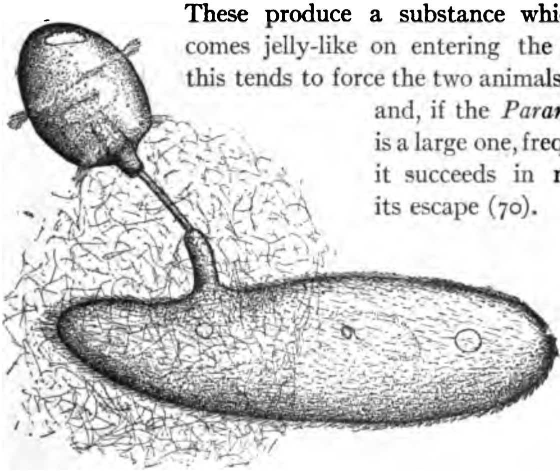


FIG. 26. *Paramecium* defending itself from an attack by a Protozoon *Didinium*. The trichocysts are discharged and mechanically force the enemy away. (From Mast in *Biol. Bul.*)

Two *contractile vacuoles* are present, occupying definite positions, one near either end of the body. They lie between the ectoplasm and the endoplasm, close to the dorsal surface, and communicate with a large portion of the body by means of a system of *radiating canals*, six to ten in number. The vacuoles grow in size by the addition of liquid which is excreted by the protoplasm into the canals and is then poured into them. When the full

size is reached, the walls contract and the contents are discharged to the exterior, probably through a pore. The two vacuoles do not contract at the same time, but alternately, the interval between successive contractions being ten to twenty seconds. The expulsion of the fluid contents of the contractile vacuoles may be seen in the following way. *Paramecia* should be mounted in water into which has been rubbed up a stick of India or Chinese ink. They then appear white against a black background. Part of the water should be withdrawn from beneath the cover glass, thus slightly compressing them. If now a specimen in profile is found and watched, the discharge produces a bright spot outside in the opaque liquid; this lasts from one to two seconds, and is then driven off by the cilia (60, Fig. 27). What has been said of the function of the contractile vacuole in *Ameba* (p. 39) applies as well to those of *Paramecium*, *i.e.* it acts as an organ of excretion and respiration, and is probably hydrostatic (50).

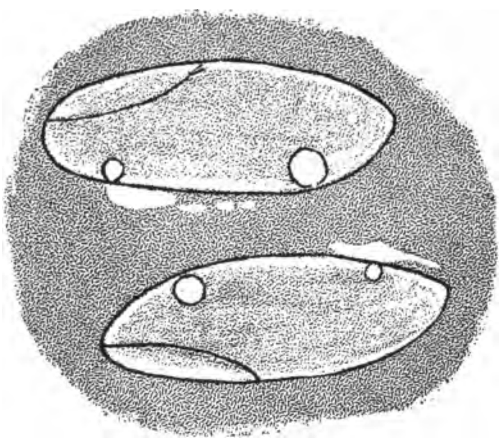


FIG. 27. *Paramecia* swimming in a solution of India ink, showing the discharge of the contractile vacuoles to the outside. (From Dahlgren and Kepner after Jennings.)

Locomotion. — The only movements of *Paramecium* that in any way resemble those of *Ameba* are seen when the animal passes through a space smaller than its shorter diameter; it will then exhibit an elasticity which allows it to squirm through. In a free field *Paramecium* swims by means of its cilia. " These are

usually inclined backward, and their stroke then drives the animal forward. They may at times be directed forward; their stroke then drives the animal backward. The direction of their effective stroke may indeed be varied in many ways, as we shall see later. The stroke of the cilia is always somewhat oblique, so that in addition to its forward or backward movement *Paramecium* rotates on its long axis. This rotation is over to the left, both when the animal is swimming forward and when it is swimming backward. The revolution on the long axis is not due to the oblique position of the oral groove, as might be supposed, for if the animal is cut in two, the posterior half, which has no oral groove, continues to revolve.

"The cilia in the oral groove beat more effectively than those elsewhere. The result is to turn the anterior end continually away from the oral side, just as happens in a boat that is rowed on one side more strongly than on the other. As a result the animal would swim in circles, turning continually toward the aboral side, but for the fact that it rotates on its long axis. Through the rotation the forward movement and the swerving to one side are combined to produce a spiral course. The swerving when the

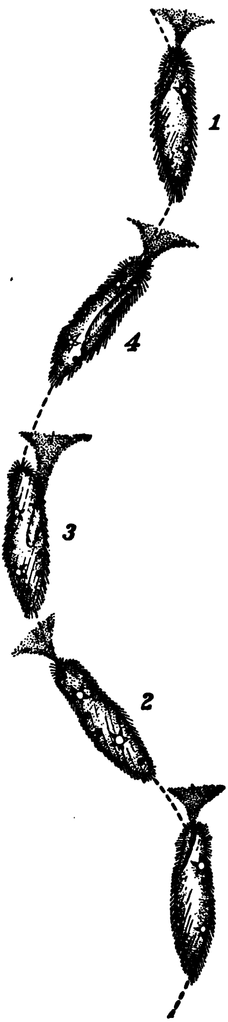


FIG. 28. Spiral path of *Paramecium*. The figures 1, 2, 3, 4, etc., show the successive positions occupied. The dotted areas with small arrows show the currents of water drawn from in front. (From Jennings.)

oral side is to the left, is to the right; when the oral side is above, the body swerves downward; when the oral side is to the right, the body swerves to the left, etc. Hence the swerving in any given direction is compensated by an equal swerving in the opposite direction; the resultant is a spiral path having a straight axis" (62, p. 44; Fig. 28).

Rotation is thus effective in enabling an unsymmetrical animal to swim in a straight course through a medium which allows deviations to right or left, and up or down. It is well known that a human being cannot keep a straight course when lost in the woods, although he has a chance to err only to the right or left.

Nutrition. — The *food* of *Paramecium* consists principally of bacteria and minute Protozoa. The animal does not wait for the food to come within its reach, but by continually swimming from place to place is able to enter regions where favorable food conditions prevail. The cilia also aid in bringing in food particles, since a sort of vortex is formed by their arrangement about the oral groove which directs a steady stream of water toward the mouth.

Figure 29 illustrates the formation of a *food vacuole* (*Ne*). Food particles that are swept into the mouth (*Mu*) are carried down into the cytopharynx (*s*) by the undulating membrane (*Mb*); they are then moved onward by the cilia lining the cytopharynx and are finally gathered together at the end of the passageway into a vacuole which gradually forms in the endoplasm (*Ne*). When this vacuole has reached a certain size, it is pinched off from the extremity of the cytopharynx by a contraction of the surrounding protoplasm, and the formation of another vacuole is begun. A food vacuole (*N*) is a droplet of water with food particles suspended within it. As soon as one is separated from the cytopharynx, it is swept away by the rotary streaming movement of the endoplasm known as *cyclosis*. This carries the food vacuole around a definite course which begins just above and behind the cytopharynx, passes backward to the posterior end, then forward near the dorsal surface to the anterior end,

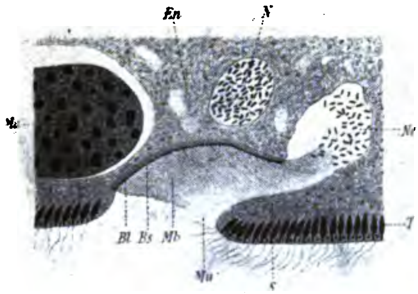


Fig. 29. A section from the region of the mouth of *Paramecium* showing the formation of a food vacuole. *En.*, endosarc; *Ma.*, macronucleus; *Mb.*, undulating membrane; *Mu.*, mouth; *N.*, food vacuole; *Ne.*, food vacuole forming; *S.*, gullet. (From Maier in *Archiv f. Protist.*)

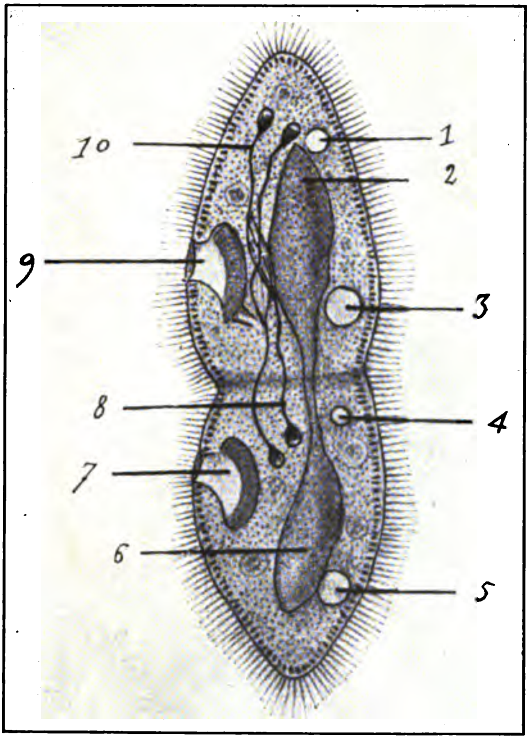


Fig. 30. Binary fission of *Paramecium aurelia.* 1, 3, 4, 5, contractile vacuoles; 2, 6, dividing macronucleus; 7, 9, gullet; 8, 10, dividing micronuclei. (From Lang's Lehrbuch.)

and finally downward and along the ventral surface toward the mouth (indicated by arrows in Fig. 23). During this journey digestion takes place.

Unlike *Ameba* a special *anal spot* (Fig. 23, *an.*) is present in *Paramecium* through which indigestible solids are discharged to the outside. This opens on the ventral surface just behind the mouth. It can be seen only when material is cast out. It is not yet known whether the anal spot is a permanent orifice whose lips are so tightly closed as to be invisible to us or whether a fresh opening is made at each discharge. The processes of digestion, absorption, dissimilation, excretion, respiration, and growth are so similar to those described for *Ameba* that they need not be considered further at this place (see pp. 49–50).

Reproduction. — *Paramecium* reproduces only by simple *binary division.* This process is interrupted occasionally by a temporary union (*conjugation*) of two individuals and a subsequent mutual *fertilization.*

Binary fission. — In binary fission the animal divides transversely (Fig. 30). The first indication of a forthcoming division is seen in the micronucleus, which undergoes a sort of mitosis (Fig. 30, *8* and *10*), its substance being equally divided between the two daughter nuclei; these separate and finally come to lie one near either end of the body. (Figure 30 shows two dividing micronuclei, since there are two of these in *Paramecium aurelia.*) The macronucleus elongates and then divides transversely (Fig. 30, *6*). The gullet produces a bud which develops into another gullet; these two structures move apart, the old gullet advancing to the ventral middle line of the forepart of the body, and the new one to a similar position in the posterior half (Fig. 30, *7* and *9*). The undulating membrane remains with the old gullet while a new one arises in connection with the new gullet. A new contractile vacuole (Fig. 30, *1*) arises near the anterior end of the body, another just back of the middle line (Fig. 30, *4*). While these events are taking place a constriction appears near the middle of the longitudinal diameter of the body; this cleavage

furrow becomes deeper and deeper until only a slender thread of protoplasm holds the two halves of the body together. This connection is finally severed and the two daughter *Paramecia* are freed from each other. Each contains both macro- and micronuclei, two contractile vacuoles, and a mouth with gullet. The entire process occupies about two hours. The time, however, varies considerably, depending upon the temperature of the water, the quality and quantity of food, and probably other factors. The daughter *Paramecia* increase rapidly in size, and at the end of twenty-four hours divide again if the temperature remains at from 15° to 17° C.; if the temperature is raised to 17°–20° C., two divisions may take place in one day (83).

Conjugation.—At a certain time in the life cycle of *Paramecium* conjugation occurs. The conditions that initiate this process are not yet known, but the complicated stages have been quite fully worked out. When two *Paramecia*, which are ready to conjugate, come together, they remain attached to each other because of the adhesive state of the external protoplasm. The ventral surfaces of the two animals are opposed, and a protoplasmic bridge is constructed between them. As soon as this union is effected, the nuclei pass through a series of stages which have been likened to the maturation processes of metazoan eggs (Chap. VII, p. 103). Reference to Figure 31 will help to make clear the following description. The micronucleus moves from its normal position in a concavity of the macronucleus (Fig. 23, *mi.*), and grows larger, its chromatin breaking up into granules which radiate from a division center at one end (Fig. 31, *a*). The nucleus then lengthens, forming a spindle, and subsequently divides into two (*b*). These immediately divide again without the intervention of a resting stage. The resultant four nuclei (*c*) have been compared to the four sperms produced by a primary spermatocyte or to an egg with its polar bodies, and the divisions are considered as the first and second maturation mitoses (see pp. 103–108). Three of the four nuclei degenerate (*d*), the fourth divides again. During this division there are no definite spindle fibers and no

longitudinal splitting of the chromosomes, but the granules of chromatin contained in the nuclei separate into two groups, one smaller (Fig. 32, A, *m. n.*) than the other (Fig. 32, A, *f. n.*).

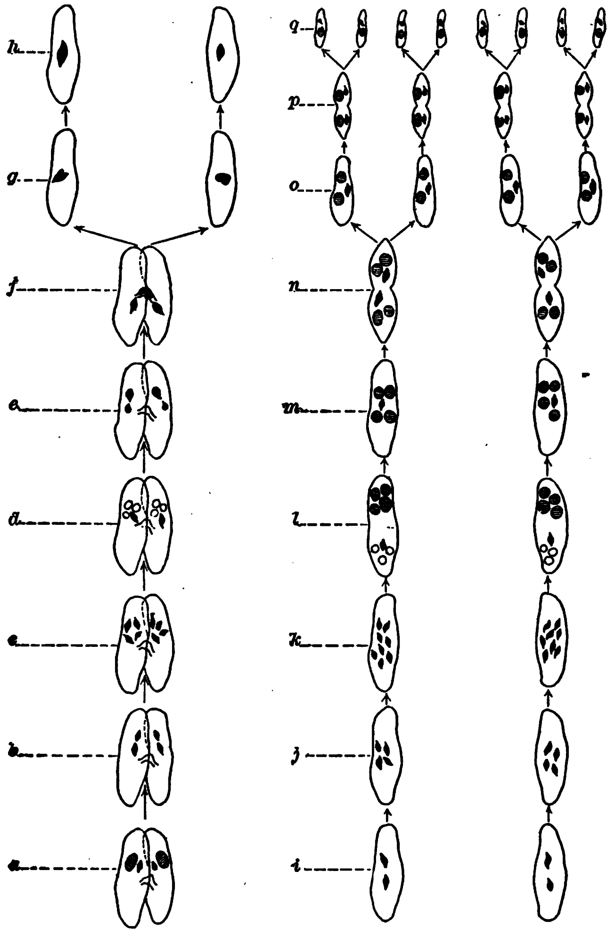


FIG. 31. Diagram showing the stages in the conjugation of two *Paramecia* and the subsequent divisions of the conjugants during the period of nuclear reconstruction. For description see text. (After Maupas.)

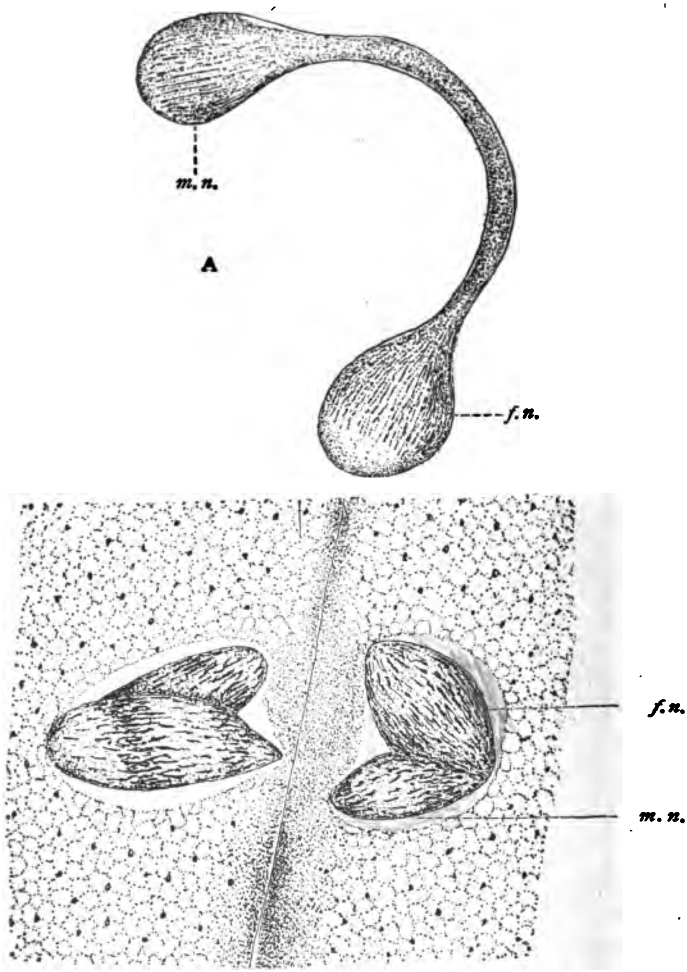


FIG. 32. Two views of the micronuclei during the conjugation of *Paramecium*. A, the spindle formed during the division of the micronucleus which results in the production of a large female nucleus (*f. n.*) and a smaller male nucleus (*m. n.*); B, the fusion of the male nucleus (*m. n.*) of one animal with the female nucleus (*f. n.*) of the other conjugant. (From Calkins and Cull. in *Archiv f. Protist.*)

These groups of chromatic material then become recognizable as distinct nuclei (Fig. 31, *e*). The smaller nucleus might be considered comparable to the male nucleus, the other the female. The male nucleus migrates across the protoplasmic bridge between the two animals (Fig. 31, *f*) and unites with the female nucleus of the other conjugant (Fig. 31, *g*; Fig. 32, B), forming a fusion nucleus (*h*). Thus is *fertilization* effected.

The conjugants separate soon after fertilization (Fig. 31, *g*). The macronucleus, which up to this time has remained at rest, now assumes a vermiform shape, breaks up into small segments, and then dissolves. The fusion nucleus of each conjugant, shortly after separation, divides by mitosis into two (*i*), these two into four (*j*) and these four into eight nuclei equal in size (*k*). Four of these forming a group near the anterior end increase in size and develop into macronuclei (*l*); the other four are grouped near the posterior end. Three of these degenerate, the fourth remains a micronucleus (*l*). The animal at this time then contains four macronuclei and one micronucleus (*m*). This micronucleus divides into two (*n*). The whole animal then divides by binary fission, each daughter cell securing two of the macronuclei and one micronucleus (*o*). The micronuclei of the two daughter cells divide again (*p*), and another binary division results in four cells each with one macronucleus and one micronucleus (*q*). An indefinite number of generations are produced by the transverse division of the four daughter cells resulting from each conjugant (71, 57, 54).

Life Cycle (53). — Enough is known of the life history of *Paramecium* to enable us to give a brief sketch of its life cycle. We must first define what we mean by an *individual*. It has been pointed out that the entire series of cells which are produced by binary division from the time of one conjugation to that of the next ought to be compared with a many-celled animal, a Metazoon (54). We have in another place (p. 14) shown that animals pass through three phases of physical activity, youth, maturity, and old age. To the period of *youth* we attribute a high degree

of vitality, rapid cell multiplication and growth, and active functions; at *maturity*, the cell division becomes less rapid, growth ends, and the organism becomes sexually mature; in *old age*, cells break down, functions become imperfect, and degeneration sets in, ending in natural death. These three stages are found in the life cycle of *Paramecium*, provided we accept the above definition of the protozoan individual; youth is characterized by rapidly dividing cells; maturity by the attainment of full size and conjugation; and old age by degeneration and natural death if conjugation is prevented.

In the stage of *youth Paramecia* do not conjugate even if many are confined in a limited space. The animals divide very rapidly at this time. They are usually almost transparent and free from reserve material of all kinds, and are able to resist adverse conditions, showing a high grade of vitality; this is due to the excess of constructive over destructive metabolism. There is no definite limit to youth. Maturity comes on imperceptibly, and mature animals can be recognized only when in some phase of sexual activity.

In a culture under continual observation a decline in the rate of reproduction indicates the approach of *maturity*. The protoplasm at this stage undergoes a change both physically and chemically; the surface layer becomes sticky, so that when two cells meet they fuse, and conjugation results. This frequently occurs in a large number of animals in a single culture at the same time and a so-called "epidemic" of conjugation may then be observed. The conjugants are smaller than the other specimens, being only .21 mm. long, while the usual length is about .3 mm. The immediate result of conjugation is apparently the rejuvenation of the conjugants.

If the *Paramecia* are kept in a constant medium, *e.g.* "hay infusion," they undergo a period of physiological depression about every three months, as shown by the decrease in their rate of division. These periods of depression are due to unknown metabolic conditions, which lessen the rapidity of division, but do not

cause the death of the animal. Semiannual periods also occur, but recovery from these does not take place if the animals are kept under constant conditions or conjugation is prevented, but the protoplasm degenerates and becomes vacuolated and the animals lose their energies and finally die.

Experiments have been performed which seem to show that in a *varied* environment neither conjugation nor death from old age necessarily occurs. Thus Woodruff (1909, 1910) has carried a culture of *Paramecia* through a period of thirty-seven months by changing the character of the medium daily. During this time there were seventeen hundred and ninety-five generations. At the end of the thirty-seventh month, the animals were normal. The cycle may thus be prolonged from six months to over thirty-seven months by employing a varied culture medium. Since in nature the stimuli derived from changes in the environment probably are present, the length of the cycle may perhaps be prolonged indefinitely.

Behavior. — *Paramecium* is a more active animal than *Ameba*, swimming across the field of the microscope so rapidly that careful observations are necessary to discover the details of its movements. As in *Ameba*, its activities are either *spontaneous*, that is, initiated because of some internal influence, or result from some *external stimulus*. This stimulus is in all cases a *change in the environment*. For example, if a drop of distilled water is added to a drop of ordinary culture water containing a number of *Paramecia*, all of the animals will enter and remain in the distilled water; they are stimulated to a certain kind of activity by the change in the composition of the water. They will soon become acclimated to their new surroundings, and will behave themselves within the distilled water in a normal manner until another change in their environment stimulates them to further reactions.

Paramecium responds to stimuli either *negatively* or *positively*. The negative response is known as the "*avoiding reaction*"; it takes place in the following manner. When a *Paramecium* receives an injurious stimulus at its anterior end, it reverses its

cilia and swims backward for a short distance out of the region of stimulation; then its rotation decreases in rapidity and it swerves toward the aboral side more strongly than under normal conditions. Its posterior end then becomes a sort of pivot upon which the animal swings about in a circle (Fig. 33). During this revolution samples of the surrounding medium are brought into the oral groove. When a sample no longer contains the stimulus, the cilia resume their normal beating and the animal moves

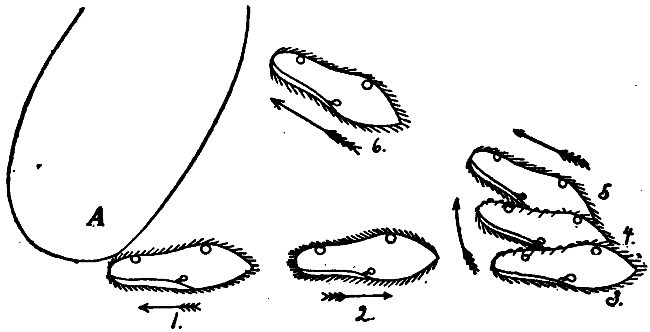


FIG. 33. Diagram of the avoiding reaction of *Paramecium*. A is a solid object or other source of stimulation. 1–6, successive positions occupied by the animal. (The rotation on the long axis is not shown.) (From Jennings.)

forward again. If this once more brings it into the region of the stimulus, the avoiding reaction is repeated; this goes on as long as the animal receives the stimulus. The repetition of the avoiding reaction is very well shown when *Paramecium* enters a drop of $\frac{1}{35}$ per cent acetic acid. In attempting to get out of the drop the surrounding water is encountered; to this the avoiding reaction is given and a new direction is taken within the acid, which of course leads to the water and another negative reaction. The accompanying Figure 34 shows part of the pathway made by a single *Paramecium* under these conditions.

Positive Reaction. — If a little acid is placed in the center of a large drop of water containing a number of *Paramecia*, all of

the animals in the drop will sooner or later encounter the acid, and having once entered are unable to escape, just as in the case described above. A group is therefore formed in the acid, illustrating what is called a positive reaction and in this case *positive chemotropism.* This experiment may be repeated using a $\frac{1}{2}$ per cent solution of common salt in which are placed a number of specimens. If a drop of $\frac{1}{10}$ per cent solution of the same chemical is now added, the *Paramecia* will swim into and directly across it, but on reaching the boundary between the two solutions on the other side of the drop, the avoiding reaction will be given. Soon the weaker solution will contain all of the animals which, having once entered, cannot escape. In many cases, as above, the passage from a strong solution to a weak solution causes no reaction. For certain substances, how-

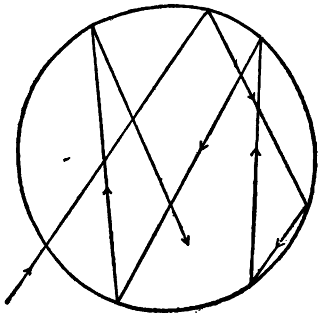


FIG. 34. Path followed by a single *Paramecium* in a drop of acid. (From Jennings.)

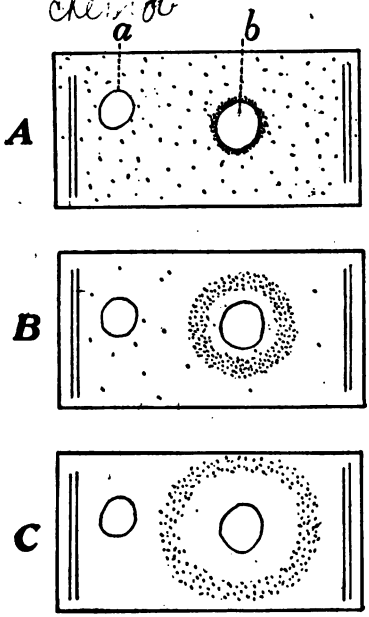


FIG. 35. Diagrams showing *Paramecia* collected about a bubble of CO_2 in the optimum concentration; *a* is a bubble of air, *b* of CO_2. A shows the preparation two minutes after the introduction of the CO_2; B, two minutes later; C, eighteen minutes later. (From Jennings.)

ever, there is a definite strength which seems to suit the *Paramecium* better than any other, and no reaction takes place on entering it. Passage from such a solution to either a weaker or a stronger calls forth the avoiding reaction. The concentration is therefore called the "*optimum*." "For each chemical there is a certain optimum concentration in which the Paramecia are not caused to react. Passage from this optimum to regions of either greater or less concentration causes the avoiding reaction, so that the animals tend to remain in the region of the optimum, and if this region is small, to form here a dense collection" (62, p. 66, Fig. 35).

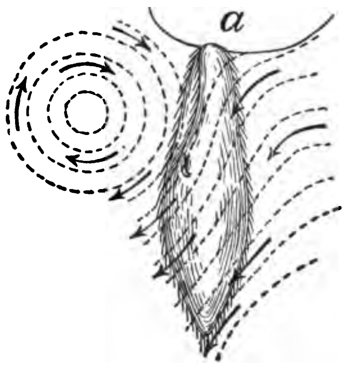


FIG. 36. *Paramecium* at rest with anterior end against a mass of bacterial zooglœa (*a*), showing the currents produced by the cilia. (From Jennings.)

Paramecia may give any one of three reactions to *contact stimuli;* the first two are negative, the third positive. (1) If *Paramecium* swims against an obstacle, or if the anterior end, which is more sensitive than the other parts of the body, is touched with a glass rod, the avoiding reaction is given. (2) When any other part of the body is stimulated in a like manner, the animal may simply swim forward. (3) Frequently a *Paramecium*, upon striking an object when swimming slowly, comes to rest with its cilia in contact with the object (Fig. 36). This positive reaction often brings the animals into an environment rich in food.

Paramecia do not respond in any way to ordinary visible *light*, but give the avoiding reaction when ultra-violet rays are thrown upon them; if unable to escape, death ensues in from ten to fifty seconds (58).

The optimum *temperature* for *Paramecium* lies, under ordinary

conditions, between 24° and 28° C. A number of animals placed on a slide, which is heated at one end, will swim about in all directions, giving the avoiding reaction where stimulated, until they become oriented so as to move toward the cooler end. This is the method of *trial and error*, that is, the animal tries all directions until the one is discovered which allows it to escape from the region of injurious stimulation.

Gravity in some unknown way causes *Paramecia* to orient themselves with their anterior ends pointed upward. This brings them near the surface of the water. If a number are equally distributed in a test tube of water, they will gradually find their way to the top (Fig. 37). The most probable theory to account for this is that the substances within the body, being of different specific gravities, move about when the animal changes its position and act as stimuli, relief being obtained only when the animal has placed its body with its long diameter perpendicular to the earth's surface and its anterior end up (68). Under certain conditions *Paramecium* exhibits positive geotropism.

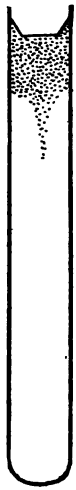


FIG. 37. *Paramecia* collected at the top of a vertical tube. (From Jennings after Jensen.)

If *Paramecia* are placed in *running water*, they orient themselves with the anterior ends upstream and swim against the current. This is probably caused by the interference of the current with the beating of the cilia, for as soon as an animal reaches a position with anterior end upstream, the water no longer tends to reverse the cilia.

Paramecia may be subjected to an *electric current* in the laboratory, but they are never influenced by it under normal conditions. A weak current causes a movement toward the cathode; a strong current reverses the direction of the beating of the cilia and causes the animals to swim backward toward the anode. Many other

interesting phenomena might be cited, but the entire subject is too complex for brief discussion.

Frequently *Paramecium* may be stimulated in more than one way at the same time. For example, a specimen which is in contact with a solid, is acted upon by gravity and may be acted upon by chemicals, heat, currents of water, and other stimuli (Fig. 38). It has been found that gravity always gives way to other stimuli, and that if more than one other factor is at work the one first in the field exerts the greater influence.

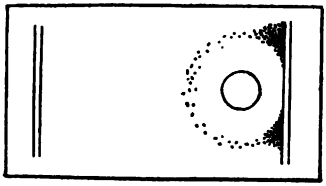


FIG. 38. *Paramecia* stimulated by a chemical and by contact at the same time. They have formed a ring about a bubble of CO_2 and have then come to rest against the glass supporting rods, forming two dense groups. (From Jennings.)

Both the spontaneous activities and reactions due to external stimuli are due to changes in the internal condition of the animal. The ***physiological condition*** of *Paramecium*, therefore, determines the character of its response. This physiological state is a dynamic condition, changing continually with the processes of metabolism going on within the living substance of the animal. Thus one physiological state resolves itself into another; this " becomes easier and more rapid after it has taken place a number of times " (62, p. 291), giving us grounds for the belief that stimuli and reactions have a distinct effect upon succeeding responses.

" We may sum up the external factors that produce or determine reactions as follows: (1) The organism may react to a *change*, even though neither beneficial nor injurious. (2) Anything that tends to interfere with the normal current of life activities produces reactions of a certain sort (' negative '). (3) Any change that tends to restore or favor the normal life processes *may* produce reactions of a different sort (' positive '). (4) Changes that in themselves neither interfere with nor assist

the normal stream of life processes may produce negative or positive reactions, according as they are usually followed by changes that are injurious or beneficial. (5) Whether a given change shall produce reaction or not often depends on the completeness or incompleteness of the performance of the metabolic processes of the organism under the existing conditions. This makes the behavior fundamentally regulatory " (62, p. 299).

Heredity in Paramecium. — Most of the complex phenomena of life are exhibited by the one-celled animals, and it is not strange to find that the offspring of the Protozoa resemble their parents. This "resemblance of child to parent" (51, p. 309) is called *heredity*. The descendants of a living organism are not exact copies of the progenitor, but differ in various minor details; " the difference between child and parent is called *variation*."(51, p. 309). *Paramecium* has been made the subject of a thorough test with regard to hereditary phenomena by Professor Jennings (65). This investigator studied and measured over ten thousand *Paramecia* which were carefully bred in the laboratory. In a " wild " lot of *Paramecia* eight distinct races were found. Each race consisted of individuals, which, though affected by their environment, maintained a certain average size which was inherited. Characteristics that were acquired by the *Paramecia* were not handed down to their offspring, but were lost when the animals were reorganized during reproduction. It is thus the " fundamental constitution of the race," and not the various external influences, which determine the characteristics of each new generation.

CHAPTER VI

OTHER PROTOZOA

1. Classification of the Protozoa

"A Protozoon is a primitive animal organism usually consisting of a single cell, whose protoplasm becomes distributed among many free living cells. These reproduce their kind by division, by budding or by spore formation, the race thus formed passing through different form changes and the protoplasm through various stages of vitality collectively known as the life cycle" (78, p. 17).

Protozoons may be separated into groups according to the presence or absence of locomotor organs and the character of these when present. Four divisions are usually recognized: (1) Rhizopoda with pseudopodia, (2) Mastigophora with flagella, (3) Infusoria with cilia, and (4) Sporozoa, which are parasitic in cells and without motile organs.

The size of Protozoa ranges within wide limits. Some are very large, for example, a parasite, *Porospora gigantea*, which lives in the alimentary canal of the lobster, reaches two thirds of an inch in length; some are just at the limit of vision with the most powerful microscopes, whereas others, like the yellow fever parasite, doubtless exist, though they have never been seen. Individuals belonging to one species vary in size according to their food conditions and age. The variations in structure and life histories of the Protozoa are so numerous as to preclude description in a book of this character. We shall therefore give an abbreviated classification of the phylum and consider typical examples under each class.

Phylum Protozoa

Class 1. Rhizopoda. Type: *Ameba proteus.* Protozoa usually simply in structure, moving by means of pseudopodia; protoplasm naked.

Order Gymnameba. Without shells.

Family Amebidæ. Pseudopodia lobose.

Genus Ameba. Ectoplasm and endoplasm distinct.

Species proteus. (Named after a sea god who had the power of assuming different shapes.)

Class 2. Mastigophora. Types: *Euglena viridis*, *Volvox globator.* Protozoa with one or more flagella; simplest forms resemble bacteria.

Order Euglenida. Large forms with one or two flagella; mouth at base of flagellum through which contractile vacuole opens to outside.

Family Euglenidæ. Elongate; one flagellum; red eye spot; green chromatophores.

Genus Euglena. Both ends contracted.

Species viridis (green).

Order Volvocina. Colonial forms with two flagella.

Family Volvocaceæ.

Genus Volvox. Colonies of many cells in a sphere.

Species globator (a ball).

Class 3. Infusoria. Type: *Paramecium caudatum.* Locomotor organs, cilia, permanent or limited to young stages; two kinds of nuclei, macronuclei and micronuclei.

Order Holotrichida. Cilia similar all over body; trichocysts present.

Family Paramecidæ. Oral groove present.

Genus Paramecium. Mouth near middle of body; pharynx short; oral groove oblique.

Species caudatum (tailed).

Class 4. Sporozoa.[1] Type: *Plasmodium vivax.* Parasitic Protozoa; no motile organs.
  Order Hemosporidia. Blood-dwelling Sporozoa.
    Genus Plasmodium.
      Species vivax (lively).

2. Euglena

(*Euglena viridis* Ehrbg.)

Euglena viridis is the animal usually selected in preparatory courses to represent the Class Mastigophora. It is found in fresh-water ponds and may appear in cultures prepared as described on page 38. It is green in color, and, though a single animal cannot be seen with the naked eye, when a great many are massed together they impart a green tint to the water.

Anatomy. — *Euglena* (Fig. 39) is a single elongated cell pointed at the posterior, and blunt at the anterior end. Two kinds of cytoplasm may be distinguished in *Euglena* as in *Ameba* and *Paramecium*, a dense outer layer, the *ectosarc*, and a central mass, the *endosarc*, which is more fluid. A thin *cuticle* is present, as in *Paramecium*, covering the entire surface of the body. Parallel thickenings of this cuticle run obliquely around the animal, making it appear *striated* (B). A little to one side of the center of the anterior blunt end of the body is a funnel-shaped depression known as the *mouth* (A, *m.*). At the bottom of this depression is an opening which leads into a short duct called the *gullet*.

[1] Only one of the protozoan types (*Plasmodium vivax*) discussed in this book is parasitic. There are, however, parasitic species in each of the classes of Protozoa. For example, the Rhizopod, *Entameba histolytica*, is held responsible for amebic dysentery; the Flagellate, *Trypanosoma gambiense*, is a blood parasite which causes sleeping sickness in Africa; and the Ciliate, *Balantidium coli*, which is found in the alimentary canal of man, is supposed to play a part in catarrhal inflamation of the intestine. Each class of Protozoa contains many other parasites of both man and the lower animals, some being apparently harmless, whereas others are dangerous and frequently fatal.

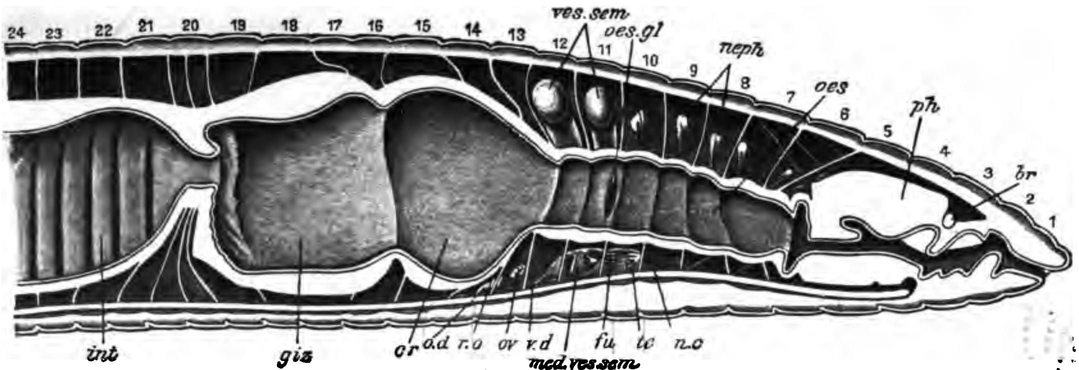


FIG. 87. Longitudinal vertical section through the anterior portion of an earthworm. *br.*, brain; *cr.*, crop; *fu.*, seminal funnel; *giz.*, gizzard; *int.*, intestine; *n.c.*, nerve cord; *neph.*, nephridia; *œs.*, œsophagus; *œs. gl.*, œsophageal gland; *ph.*, pharynx. (From Parker and Haswell after Marshall and Hurst.)

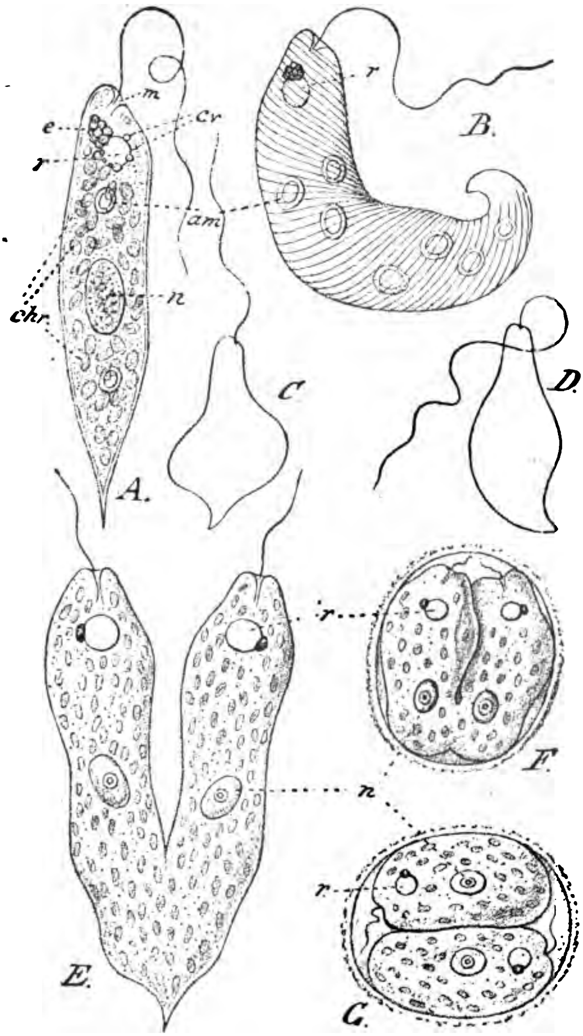


FIG. 39. *Euglena viridis.* A, view of free-swimming specimen showing details of structure; B, another animal showing change of shape and striations; C and D, outlines showing stages of contraction; E, reproduction by longitudinal fission; F and G, division within a cyst: *am.*, pyrenoids with sheaths of paramylum; *chr.*, chromatophors; *c.v.*, contractile vacuoles; *e.*, stigma; *m.*, mouth; *n.*, nucleus; *r.*, reservoir. (A–D from Bourne; E–G, from Bourne after Stein.)

This in turn enters a large spherical vesicle, the *reservoir* (*r.*), into which several minute *contractile vacuoles* (A, *c. v.*) discharge their contents.

A conspicuous structure in *Euglena* is the *red eye spot* or *stigma* (Fig. 39, A, *e.*). This is placed near the inner end of the gullet close to the reservoir. It consists of protoplasm in which are embedded a number of granules of *hæmatochrome.* The anterior end of the body of *Euglena* is said to be more sensitive to light than any other part, and it is supposed by some that the stigma functions as a rather primitive visual organ. This view is made probable by the presence of lens-like *paramylum* grains just anterior to it. The hæmatochrome also has many of the characteristics of the pigments in the eyes of higher organisms. If kept in the dark, *Euglena* soon loses its red pigment. A recent view is that the hæmatochrome shades a sensitive particle of protoplasm.

Euglena contains a single oval *nucleus* (Fig. 39, *n.*) lying in a definite position a little posterior to the center of the body. It has a distinct membrane, and contains a central body which has been called a *nucleolus* (E), but probably is not, since it functions as a division center during mitosis.

Euglena derives its green color from a number of oval disks suspended in the protoplasm. These are known as *chromatophores* (Fig. 39 A, *chr.*). They are arranged about a collection of granules situated in the center of the body, and contain chlorophyll, which is diffused throughout their protoplasmic contents. They manufacture food by a process common in green plants but rare in animals, called *photosynthesis* (see p. 18 and Fig. 3). The chlorophyll is able, in the presence of light, to break down the carbonic acid (CO_2), thus setting free the oxygen, and to unite the carbon with water, forming a substance allied to starch called *paramylum* (A and B, *am.*). If specimens are kept in good light continually, a large amount of paramylum will be stored up for future use, being laid down around some granules of proteid substance near the center of the body. These granules are called

pyrenoids. Both the pyrenoids and chromatophores are permanent cell structures and increase in number by division and not by the origin of new ones from the other parts of the body.

Locomotion. — *Euglena* changes its shape frequently, becoming shorter and thicker, and shows certain squirming movements. These prove that it possesses considerable *elasticity*, since the normal shape is regained if enough water is present. Often in a favorable specimen, a thread-like structure may be seen projecting from the anterior end of the body and bending to and fro, drawing the animal after it. This is the *flagellum*. It arises from a number of branching root-like fibrils within the body, passes through the wall of the mouth depression, and extends forward to a distance often equal to the length of the animal. The part of the flagellum outside of the body is composed of four contractile fibrils which are wound together spirally (Fig. 25). The contraction of these fibrils is supposed to produce all of the movements characteristic of this structure (56). If the flagellum cannot be seen in the living animal, a little iodine placed under the cover glass will help to bring it out.

Nutrition. — Although *Euglena* has a mouth and gullet, it is very doubtful if any food is taken in. *Food* is manufactured as in green plants, by the aid of the chlorophyll in the chromatophores. This mode of nutrition is known as *holophytic*. That all the food necessary for the life of the animal is not procured in this way is shown by the fact that the animal is able to live in the dark for over a month, whereas chlorophyll demands light before the production of paramylum is possible. This seems to indicate that organic substances in solution are absorbed through the surface of the body, that is, *saprophytic* nutrition supplements the holophytic. The nutrition of *Euglena* differs from that of the majority of animals, since the latter live by ingesting solid particles of food and are said to be *holozoic*.

Encystment. — Occasionally *Euglenæ* are found which have become almost spherical and are surrounded by a rather thick gelatinous covering which they have secreted. Such an animal

is said to be encysted (Fig. 39 F and G). In this condition periods of drought are successfully passed, the animals becoming active when water is again encountered. Usually in cultures brought into the laboratory many cysts are found on the sides of the dish.

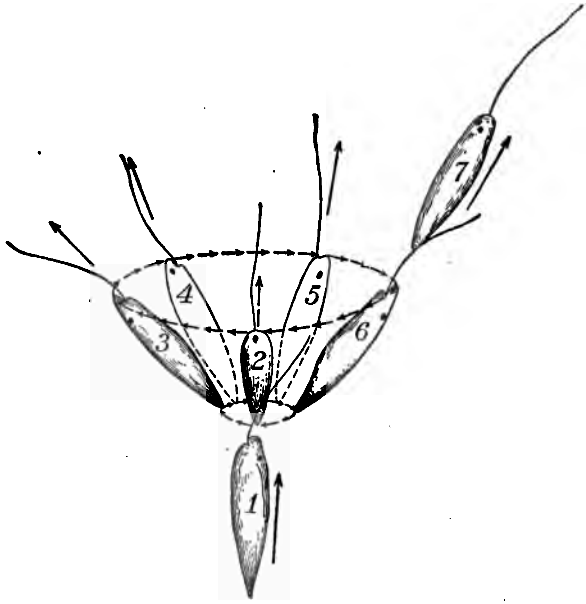


FIG. 40. Diagram of the reaction of *Euglena* when the light is decreased. The organism is swimming forward at 1; when it reaches 2 it is shaded. It thereupon swerves toward the dorsal side, at the same time continuing to revolve on the long axis, so that its anterior end describes a circle, the *Euglena* occupying successively the positions 2–6. From any of these it may start forward in the directions indicated by the arrows. (From Jennings.)

Encystment frequently takes place without any apparent cause, the animal resting in this condition for a time and then emerging again to its free swimming habit. Before encystment the flagellum is thrown off, a new one being produced when activity is again resumed.

Reproduction. — Reproduction in *Euglena* takes place by *binary longitudinal division* (Fig. 39 E). The nucleus divides by a primitive sort of mitosis. The body begins to divide at the anterior end. The old flagellum is retained by one half, while a new flagellum is developed by the other. Often division takes place while the animals are in the encysted condition. One cyst usually produces two *Euglenæ* although these may divide while still within the old cyst wall, making four in all, while recent observers have recorded as many as thirty-two young flagellated *Euglenæ* which escaped from a single cyst.

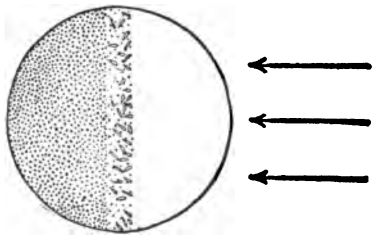


FIG. 41. Diagram showing the reaction of *Euglenæ* to light. The light comes from the direction indicated by the arrows, while the opposite side of the vessel is shaded, as indicated by the dots. The *Euglenæ* gather in the intermediate region across the middle. (From Jennings.)

Behavior. — *Euglena* swims through the water in a spiral path. The effect of this course is, as we found in *Paramecium* (p. 64), the production of a perfectly straight course through the trackless water. When stimulated by a change in the intensity of the light, *Euglena*, in the majority of cases, stops or moves backward, turns strongly toward the dorsal side, but continues to revolve on its long axis. The posterior end then acts as a pivot while the anterior end traces a circle of wide diameter in the water. The animal may swim forward in a new direction from any point in this circle. This is the *avoiding reaction* (Fig. 40).

Euglena is very sensitive to light and is a favorable object for the study of *phototropism.* It swims toward an ordinary light such as that from a window, and if a culture containing *Euglenæ* is examined, most of the animals will be found on the side toward the brightest light. This is of distinct advantage to the animal, since light is necessary for the assimilation of carbon dioxide

by means of its chlorophyll. *Euglena* will swim away from the direct rays of the sun. Direct sunlight will kill the organism if allowed to act for a long time. If a drop of water containing *Euglenæ* is placed in the direct sunlight and then one half of it is shaded, the animals will avoid the shady part and also the direct sunlight, both of which are injurious to them, and will remain in a small band between the two in the light best suited for them, that is, their *optimum* (Fig. 41). By shading various portions of the body of a *Euglena* it has been found that the region in front of the eye spot is more sensitive than any other part. It should be noted that when *Euglena* is swimming through the water it is this anterior end which first reaches an injurious environment; the animals give the avoiding reaction at once, and are thus carried out of danger.

3. Plasmodium

(*Plasmodium vivax* Grassi)

The Sporozoa are parasitic Protozoa and are responsible for many of the most malignant animal diseases. One of the best known of all Sporozoons is *Plasmodium vivax*, which causes Malarial Fever. This minute animal was discovered in the blood of malaria patients by a French military doctor, Laveran. It was suggested by this investigator, in 1891, that the parasite is probably transmitted from man to man by some blood-sucking insects, and this hypothesis was proved to be correct by the work of Major Ross in 1899. Not only was it demonstrated that malaria is spread by insects, but it was proved that human beings can only become infected by the bite of a mosquito belonging to the genus *Anopheles*. The two most common genera of mosquitoes are *Culex* and *Anopheles*. One of the easiest methods of distinguishing one from the other is by observing their position when at rest. It will be found that the harmless *Culex* holds its abdomen approximately parallel with the surface on which it alights, whereas the abdomen of *Anopheles* is held at an angle.

There are three well-known types of malaria; these may be

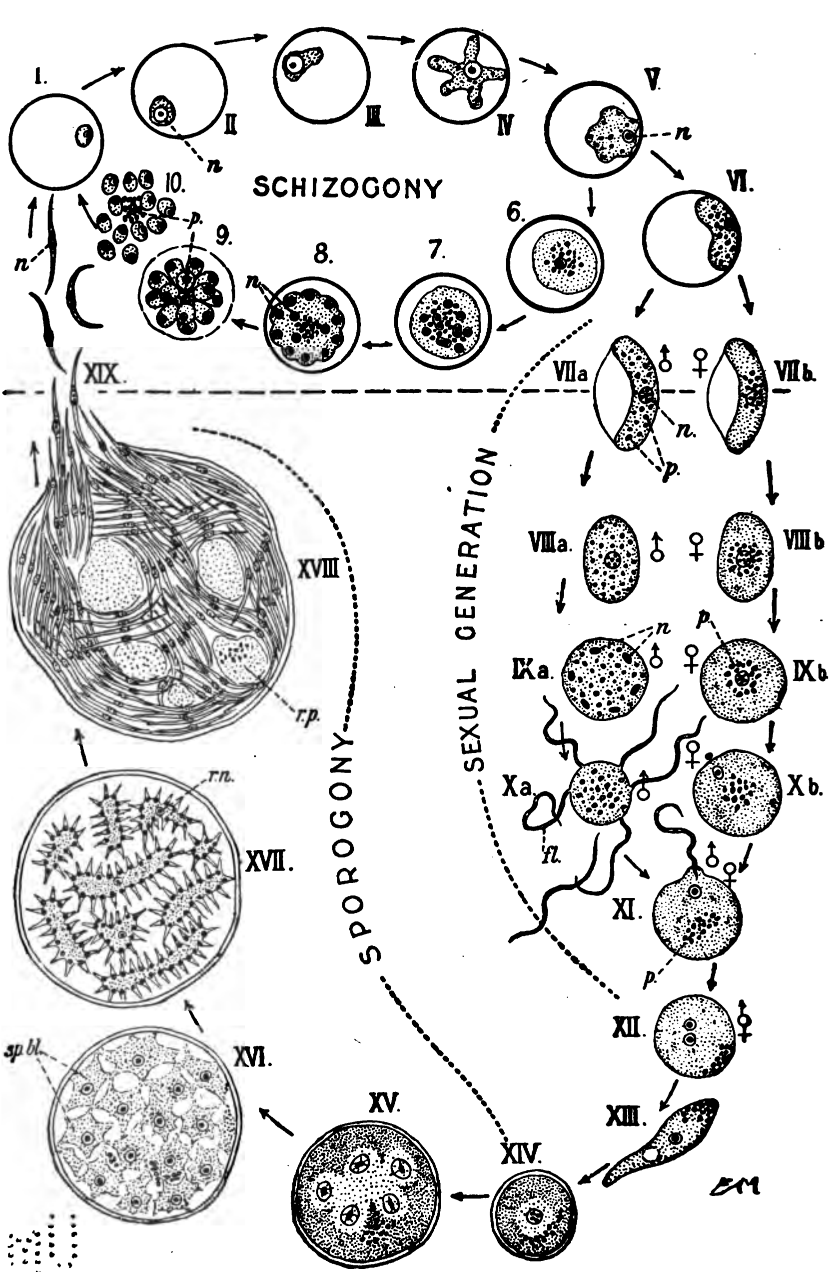


FIG. 42. Diagram illustrating the life history of the Malarial Fever parasite. The stages shown above the line of dashes are passed through in the blood of a human being; those below the line, in the body of an *Anopheles*, mosquito. For explanations of the stages, e pages 89–91. (From Minchin in Lankester's Treatise after various authors.)

recognized by the intervals between successive chills. (1) *Tertian fever*, caused by *Plasmodium vivax*, is characterized by an attack every forty-eight hours; (2) *quartan fever*, caused by *Plasmodium malariæ*, with an attack every seventy-two hours, and (3) *estivo-autumnal* or *pernicious fever*, caused by *Plasmodium falciparum*, produces attacks daily or more or less constant fever. The life histories of these three species of *Plasmodium* differ very slightly one from another. *Plasmodium vivax* has been selected for presentation here as a type of the group Sporozoa. The various stages that occur during the life cycle of this parasite offer a mass of detail that can only be adequately discussed in a larger work, so we shall simply give a brief outline of the chief phases.

Tertian fever is transmitted by diseased female mosquitoes only. The mouth parts of these insects are adapted for piercing. When they have been thrust into the skin of the victim, a little saliva is forced into the wound. This saliva contains a weak poison which is supposed to prevent the coagulation of the blood and thus the clogging of the puncture. Blood is sucked up by the mouth parts into the alimentary canal of the mosquito; this process occupies from two to three and a half minutes. With the saliva a number of parasites, which were stored in the salivary glands of the insect, find their way into the wound. Constant reference to Figure 42 will make the following description clear.

At the time of their entrance the parasites are slender boat-shaped cells pointed at both ends, and are called *sporozoites* (XIX). These sporozoites immediately penetrate the red blood corpuscles by means of wriggling movements. Inside of the blood corpuscle the sporozoite becomes ameboid in shape, and begins to feed on the surrounding protoplasm (I). As it grows larger a vacuole develops, giving it a ringlike appearance (II and III). When fully grown the parasite almost completely fills the blood corpuscle and its ameboid movements cease (IV, V, and 6). Within its body can be seen a number of dark brown granules

called *melanin* (9 and 10, *p.*); these are waste matters that have accumulated during the growth period, being modified products of the digestion of hæmoglobin.

Reproduction now takes place by a p ocess termed *schizogony* (I–V and 6–10), the parasite after it enters the blood corpuscle, being known as a *schizont.* During this process the nucleus divides a number of times without the intervention of cell walls until from twelve to sixteen daughter nuclei are present (8). Each nucleus, with part of the surrounding cytoplasm, is then cut off from its fellows, resulting in the production of a number of small cells, called *merozoites*, inclosed in the membrane of the corpuscles (9). The melanin granules are not included in the daughter cells, but remain in the center of the mother parasite (9, *p.*). The merozoites finally break through the walls of the corpuscle and escape into the blood plasma. The melanin granules are also liberated at this time (10, *p.*); they are carried by the blood to the liver, kidney, spleen, lungs, or brain, frequently resulting in the pigmentation and hypertrophy of these organs. An attack of fever coincides with the liberation of the merozoites, and the interval between the penetration of a blood corpuscle and the production of merozoites is termed the period of incubation. This period in *Plasmodium vivax*, as stated above, is forty-eight hours. All the merozoites simultaneously attack other corpuscles (10 to I), producing the chill which is a symptom of malaria.

Several asexual cycles like that just described are passed through; but finally, for some unknown reason, the merozoites develop into *sexual phases* (VI–XII). Part of them, named *macrogametocytes* (VII, *b.*) become capable of producing a single *female gamete* or *macrogamete* (*X*, *b.*), while the rest become *microgametocytes* (VII, *a.*), each capable of producing as many as eight *male elements* or *microgametes* (*X*, *a.*). The gametocytes cannot produce gametes within the human body but must first be sucked up into the alimentary canal of an *Anopheles* mosquito. Here all stages of the parasite except the gametocytes are di-

gested; the latter seem stimulated by the digestive juices to further development.

The *macrogametocyte* now goes through the process of *maturation* (see p. 105), one small polar body being extruded (X, *b.*); what remains is a large macrogamete. The nucleus of the *microgametocyte* (IX, *a. n.*) divides into eight daughter nuclei which migrate to the periphery and enter the long protoplasmic processes that have, in the meantime, been thrust out from the cell (X, *a.*). These flagelliform nucleated processes then break away from the microgametocyte as male cells, microgametes or spermatozoa, and move about until they encounter a macrogamete with which they fuse (XI). What remains of the microgametocyte slowly disintegrates. Only one microgamete fuses with a macrogamete in the process of *fertilization.*

The result of this fusion is a *zygote* which has been given the name *oökinet* (XII). This zygote becomes spindle-shaped (XIII) and makes its way by vermiform movements to the epithelial cells lining the alimentary canal of the mosquito; it penetrates these and reaches the underlying tissues. Here it grows rapidly; the nucleus divides, forming many daughter nuclei, and by the sixth day as many cells are produced as there are nuclei (XIV–XVI). Each cell is a *sporoblast* (XVI, *Sp. bl.*). The sporoblast forms by division a number of germs, the *sporozoites* (XVII–XVIII); these mature in about fourteen days and are then set free into the body cavity of the mosquito (XVIII–XIX). From here they are carried by the circulating plasma to all parts of the body, finally collecting in the anterior region. They make their way into the salivary glands, and are then ready to pass into the blood of the human being at the time the mosquito makes its next meal.

Malarial fever is not present wherever *Anopheles* is found; for example, *Anopheles* is common in England, but no malaria occurs there. It is supposed that mosquitoes may become immune to all kinds of blood parasites. A mosquito that is able to digest the parasite becomes harmless to man. The mosquitoes of the

genus *Culex* are able to digest all stages of ***Plasmodium vivax***, and are therefore immune. On the other hand, this mosquito does not digest all of the organisms of the malaria which attacks birds and thus becomes infected and is the means of transmitting the fever from one bird to another.

Quinine is the remedy commonly used against the malarial parasite. It acts directly upon the younger stages of the organism, causing death.

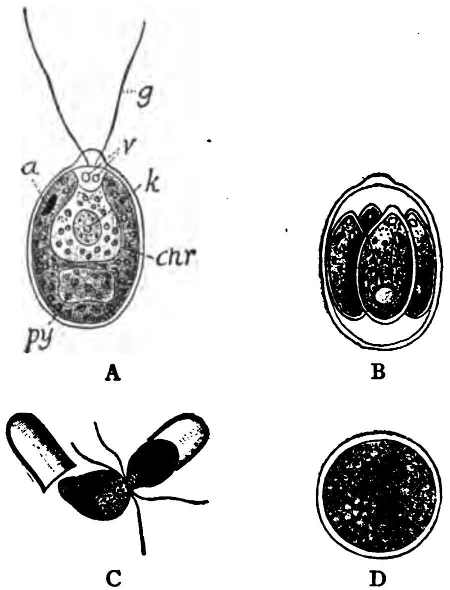


FIG. 43. *Chlamydomonas*. A, single vegetative cell: *a*, stigma; *chr.*, chromatophor; *g.*, flagellum; *k.*, nucleus; *py.*, pyrenoid; *v.*, vacuoles. B, Four daughter cells still within the cell wall of the parent; C, the union of two gametes; D, zygote. (From Oltmanns.)

4. VOLVOX GLOBATOR AND ITS ALLIES

Certain organisms which lie on the borderland between plants and animals are peculiarly favorable for illustrating how a multicellular animal like *Volvox* (Fig. 46) may have evolved from a single-celled ancestor. These organisms belong to the Family Volvocaceæ. They are important not only for their phylogenetic significance but also because they illustrate the *evolution of sex*. Starting with the unicellular *Chlamydomonas*, the line of evolution passes through *Spondylomorum*, *Pandorina*, *Eudorina*, and finally ends with *Volvox* (76).

Chlamydomonas (Fig. 43) is found in ponds, ditches, and rain pools. It is oval in shape, green in color, and swims about by means of two flagella (*g*) which project from one end (Fig. 43 A). The central mass of protoplasm is covered by a definite wall of cellulose. Within the cells are a nucleus (*k*), two small contractile vacuoles (*v*), a large pyrenoid (*py*), a red pigment spot (*a*), the stigma, and chromatophors (*chr*).

Reproduction takes place in two ways. First, a cell comes to rest and its contents divide into two, four or eight daughter cells which assume the characteristics of the parent organism and lead a separate existence (Fig. 43 B). Second, a cell may divide into from sixteen to sixty-four cells without walls; these are smaller than the vegetative cells, but resemble one another. They are known as gametes. The gametes fuse in pairs (Fig. 43 C), forming spherical bodies with heavy walls called zygotes (D); after a period of rest, the contents of the zygotes divide into a number of parts which escape from the walls and grow into vegetative cells.

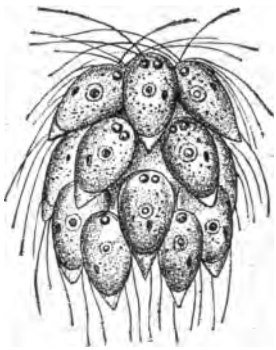


FIG. 44. *Spondylomorum*. (From Oltmanns.)

Spondylomorum (Fig. 44) differs from *Chlamydomonas* in a number of particulars, the most noticeable being its *colonial habit*. Specimens may be found in situations similar to those cited for *Chlamydomonas*. When brought into the laboratory they collect at the side of the culture dish nearest the window, reacting positively to light of moderate intensity. Sixteen cells form a colony; they are arranged in four rows of four each, alternating, as shown in Figure 44. Each cell appears to be exactly like every other cell; it possesses four flagella and has a chlorophyll body which enables it to manufacture its own food. All of the somatic functions are carried on by each cell independently

of all the others. Reproduction likewise takes place in each cell.

So far as known *reproduction* of only one kind occurs; this is the simultaneous longitudinal division of each cell into two, four, eight, and finally sixteen daughter cells. These daughter cells do not separate as do the daughter cells when *Chlamydomonas* divides, but remain fastened together by a gelatinous matrix. Each cell of the mother colony thus produces a daughter colony of sixteen cells. If another kind of reproduction does take place, it is probably by the union of similar gametes forming a zygote similar to that of *Chlamydomonas.*

Pandorina morum (Fig. 45) is likewise a colonial form found in fresh-water ponds. It consists of sixteen cells which are held together by a gelatinous matrix, part of which is secreted by each cell (I). Each cell possesses one pair of flagella and an eye spot, and contains chlorophyll. It is thus enabled to carry on all of the processes necessary to sustain life, to grow, and to reproduce.

Reproduction in this species takes place in two ways. First, as in *Spondylomorum,* each cell may divide to form two, four, eight, and then sixteen daughter cells, which become a new colony (Fig. 45, II). The new colonies escape from the mother colony by the dissolution of the gelatinous envelope, and swim away to lead a separate existence. This method of reproduction occurs repeatedly, but finally *conjugation* is inaugurated. Each of the sixteen cells of the mother colony produces by division sixteen or thirty-two daughter cells. Each daughter cell develops flagella and separates not only from the mother colony, but from its sister cells in the daughter colony (III). This separation results from a solution of not only the gelatinous envelope of the mother colony but also that which holds the daughter cells together. These isolated cells are known as *gametes.* The gametes are not all of the same size, some being larger than others. When two gametes meet, they become fastened together by their anterior ends and gradually fuse (IV–V). The fused cells constitute a *zygote,* containing two eye spots and bearing four flagella (V). The flagella

are soon cast off and the zygote sinks to the bottom of the pond where it secretes a thick red wall about itself (VI–VII). It remains in this condition throughout the summer, becoming dry when the pool of water in which it lives evaporates. In the autumn activity is again resumed. The zygote produces from

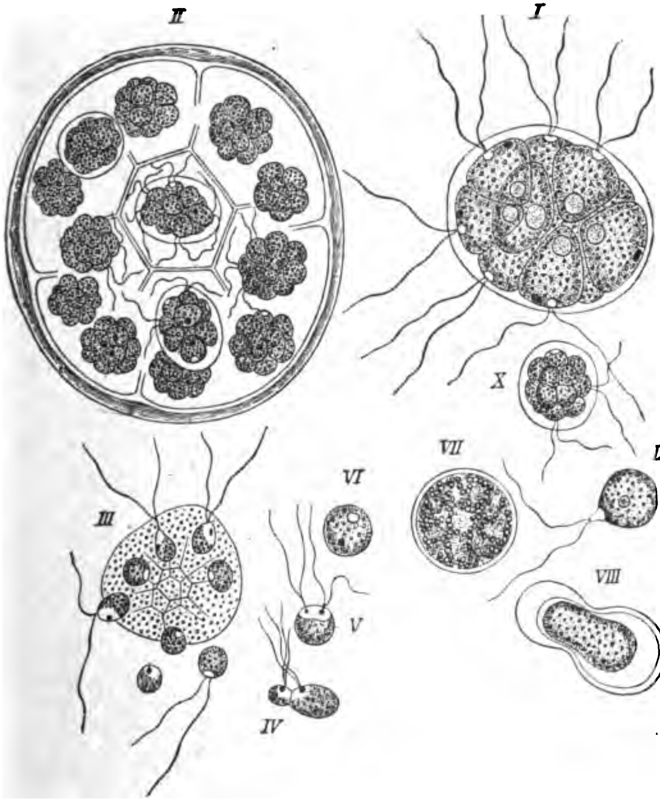


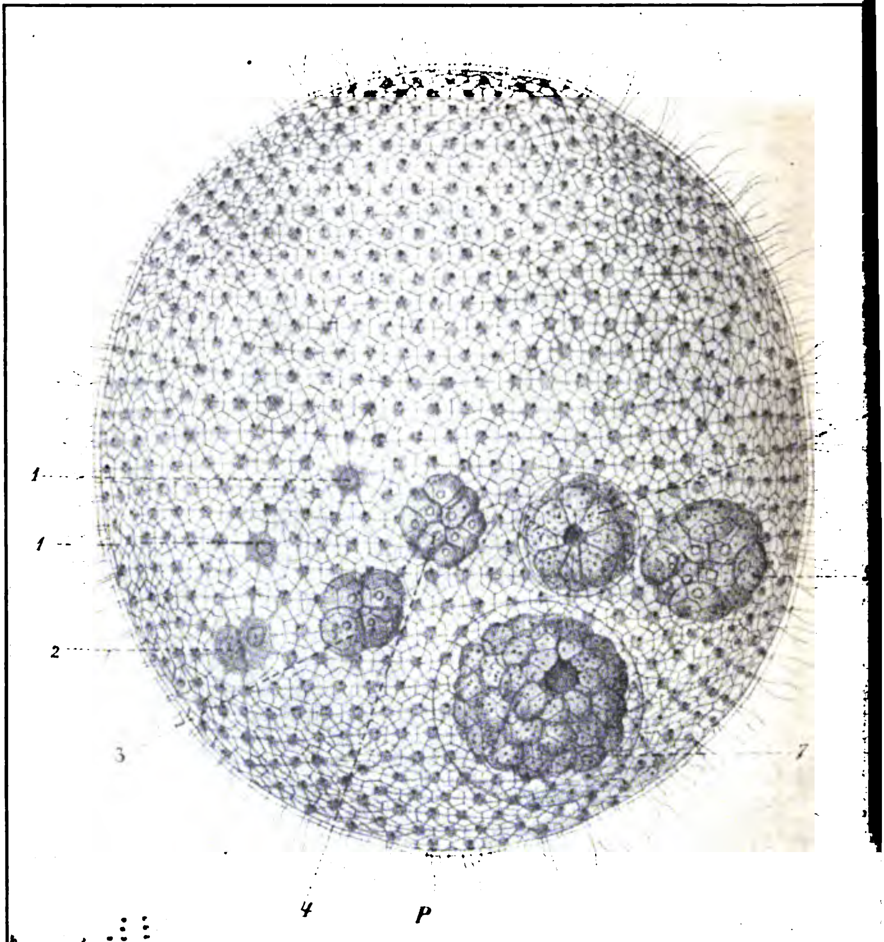
FIG. 45. *Pandorina morum.* I, vegetative colony; II, formation of daughter colonies; III, escape of gametes; IV, V, VI, VII, fusion of two gametes to form a zygote; VIII, IX, production of swarm spores by a zygote; X, vegetative colony formed by a swarm spore. (From Oltmanns.)

one to three *swarm spores* which escape from the cyst and swim away (VIII–IX). Each swarm spore develops at once by binary division a new colony of sixteen cells (X).

The gametes of *Pandorina* are not equal in size as in *Chlamydomonas*, but appear to be of two kinds, some larger than others. Where such a condition exists the smaller gametes are called *male cells* or *sperms*, the larger, *female cells* or *eggs*. *Sexual reproduction* consists in the union of a male cell with a female cell, and certain investigators believe the larger gametes of *Pandorina* tend to fuse with the smaller. If this is true, we have in this organism the beginning of the evolution of sexual reproduction.

In **Eudorina elegans**, another member of the family Volvocaceæ, this distinction between male and female gametes is more clearly seen. *Eudorina* is a spherical colony containing thirty-two, rarely sixteen cells which resemble the cells of *Pandorina*. *Reproduction* by simple division takes place as in *Pandorina*. This cannot go on indefinitely, for finally some colonies are found whose cells have grown larger than usual. These are female colonies, and the cells are *macrogametes*. Other colonies produce microgametes; each of the thirty-two cells of these male colonies divides, producing a flat plate of sixteen or thirty-two spindle-shaped *microgametes* each with a pair of flagella extending from its anterior end. When a plate of microgametes encounters a colony of macrogametes it becomes attached to it, the microgametes separate from the plate and make their way through the gelatinous envelopes of the macrogametes, thus *fertilizing* them and forming *zygotes*.

It should be noted that the organization of *Eudorina* is more complex than that of the other three species considered, and that this advance in complexity is gradual. In *Eudorina*, also, the small microgametes are perfectly distinct from the large macrogametes, and fertilization always consists in the union of a macro- with a microgamete. This size difference is not so evident in *Pandorina*.



A

FIG. 46. *Volvox globator*. A, a colony reproducing by means of parthenogonidia; 1–7, vari
stages in the division of a germ cell to form a daughter colony. (From Lang.)

Finally in **Volvox globator** (Fig. 46), the specialization of the body cells as well as the reproductive cells reaches a stage in which certain cells are set apart for reproductive purposes while others carry on the vegetative functions of the colony.

Volvox is a colonial organism found in fresh-water ponds. It can easily be seen with the naked eye, being from .2 to .7 mm. in diameter. It may be compared with a hollow rubber ball, since it is a hollow sphere consisting of a single peripheral layer of cells embedded in a gelatinous matrix. Each of the twelve thousand cells which may be present has a thick envelope separating it from the surrounding cells; mutual pressure gives these a hexagonal shape (Fig. 46 A). Strands of protoplasm connect each cell with the six cells that surround it (Fig. 46 C); *physiological continuity* is thus established between the cells, a condition not found in the colonies previously described. Most of the cells contain an eye spot, chlorophyll, a contractile vacuole, and two flagella. These are called "*body*" or *somatic cells*. They serve to propel the colony through the water and to carry on nutritive processes, but are incapable of reproducing new colonies, although in young colonies they divide, giving rise to daughter cells like themselves. The production of daughter colonies is accomplished by special reproductive cells which are set aside for this purpose.

Reproductive cells give rise to new colonies in two ways: (1) asexually, and (2) sexually. The *asexual* method is as follows. Certain cells of the colony are larger than others and lack flagella (Fig. 46 A, *1*); a number of these in one colony increase in size, and divide by simple fission into a great number of cells, producing new colonies without being fertilized (A, *1–7*). The cells that act in this way are named *parthenogonidia*. The colonies derived from them drop into the central cavity of the mother colony, where they swim about for a short time, finally escaping through a chance opening in the wall.

After colonies have been produced in this manner for several generations the *sexual* method of reproduction may be observed (Fig. 46 B). Colonies are found which contain as many as fifty

of the larger cells without flagella. Some of these grow larger and may be recognized as *female cells* or *macrogametes* (*o*); others produce by simple division a flat plat, containing about one hundred and twenty-eight spindle-shaped *male cells* or *microgametes* (*s*). These escape into the central cavity and fuse with the macrogametes. The *zygote* thus formed secretes a surrounding wall consisting of two layers, the outer of which is reddish in color and covered with short spines. In this condition the winter is passed. The following spring the zygote breaks out of the wall and by division produces a new colony. The smaller somatic cells contained in the mother colony fall to the bottom and disintegrate as soon as the new colonies produced by the fertilized germ cells have escaped.

In *Volvox*, *true somatic cells* are encountered for the first time, that is, cells which function only vegetatively and are unable to reproduce the colony. In the other forms described every cell has the capacity of reproducing the whole. *Volvox* also contains *true germ cells*, that is, cells that have given up nutritive functions to carry on reproduction. Furthermore, a clear case of *natural death* occurs in the somatic cells when they fall to the bottom of the pond and disintegrate. The bodies of higher animals consist of many cells which may be separated into somatic and germ cells. The latter are either male or female. In most cases a fusion of a male cell with a female cell is necessary before a new animal can be reproduced. At any rate, some of these germ cells maintain the continuation of the species by producing new individuals while the somatic cells perish when the animal dies.

The Germ Plasm Theory. — Figure 47 illustrates the theory of the continuity of the germ-plasm which is held by most zoologists at the present time. By germ-plasm is meant that part of the protoplasm which is set aside for reproductive purposes and determines that the offspring shall resemble their parents; this special material is stored in the germ cells. In the spring of the year the *Volvox* race is represented by fertilized eggs (zygotes) only; each of these divides, producing an animal con-

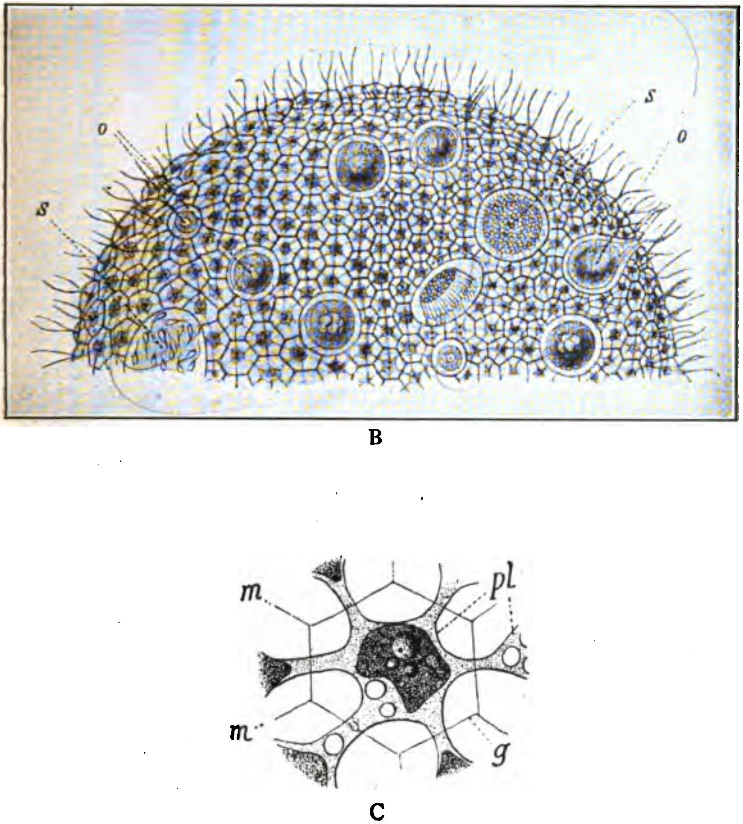


FIG. 46. *Volvox globator.* B, a colony reproducing by means of eggs and sperms: *o.*, eggs; *s.*, sperms. (From Lang.) C, a single cell showing protoplasmic connections, *pl.*, cell protoplasm; *g.*, jelly; *m.*, lines showing limits of cell envelope. (From Oltmanns after various authors.)

taining as many as twelve thousand cells, a few of which are reproductive cells and contain the germ-plasm. In the autumn the germ-plasm is segregated in the eggs and spermatozoa, which fuse two by two, an egg with a sperm, producing zygotes. The somatic or body cells fall to the bottom and die, but the zygotes live through the winter and germinate in the spring, thus assuring the continued existence of the race.

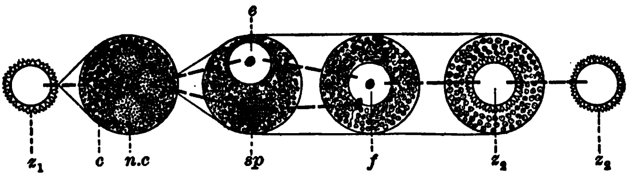


FIG. 47. Diagram to illustrate the theory of the continuity of the germ-plasm by means of *Volvox*. The fertilized egg or zygote (z_1) produces by division in the spring a colony (*c*) containing a great many cells, some of which are set aside for reproductive purposes. These produce new colonies (*n.c.*) during the summer by the asexual method. Male cells (spermatozoa, *sp*) and female cells (eggs, *e*) are also formed. In the autumn the body dies, but the fertilized germ cells (z_2) produced by the union of eggs and spermatozoa (*f*) survive the winter, dividing to form new colonies the next spring.

Certain processes in the development of the fertilized eggs of some of the more complex animals strengthen the belief in the passage of the germ-plasm from one generation to another, and seem to indicate that the body is not the producer of the germ cells, but is simply a vehicle which carries them about until they reach maturity. The body then dies and disintegrates, the important function of reproduction, and consequently the survival of the race, being left in charge of the mature germ cells.

CHAPTER VII

AN INTRODUCTION TO THE METAZOA

1. Cellular Differentiation — Tissues

There is no sharp line between the Metazoa and Protozoa. We have seen (Chap. VI) that the Volvocaceæ, which are often included in the Phylum Protozoa, are many-celled colonies, the cells of which are either entirely independent, as in *Spondylomorum* (Fig. 44), or are connected by protoplasmic strands, as in *Volvox* (Fig. 46). Here the cells of the colony have ceased to be independent, but have united to form a distinct body which carries on nutritive processes, produces germ cells, and then dies. The cells of this body are called somatic cells. Their functions are locomotor and nutritive, but not reproductive. Such an aggregation of cells is known as a tissue. A *tissue* is an association of similar cells originating from a particular part of the embryo and with special functions to perform. In *Volvox* there is only one kind of tissue; in some of the simple Metazoa there are two kinds of tissue resulting from the differentiation of the somatic cells; in the majority, however, there are at least three and usually more. The many different kinds of tissue in the Metazoa may be classified according to their structure and functions into four groups.

(1) **Epithelial tissue** (Fig. 48 A, B) consists of cells which cover all the surfaces of the body both without and within. In the simpler animals this is the only kind of tissue present. The somatic cells of *Volvox* may be considered epithelium. In the more complex animals epithelial cells become variously modified because they are the means of communication between the organism and its environment; nutritive material passes through

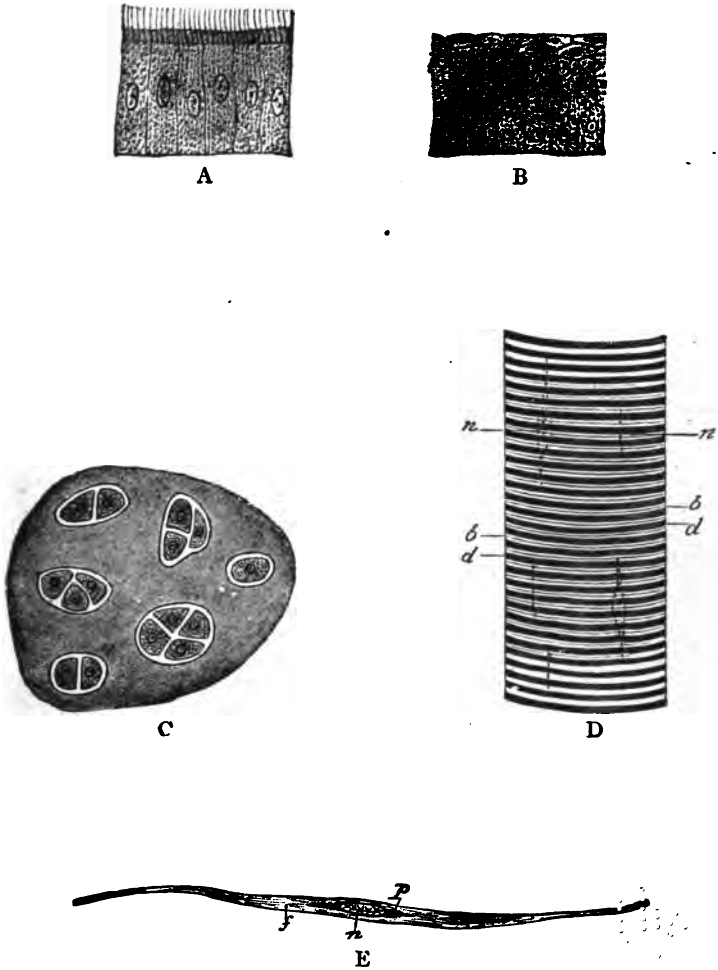


FIG. 48. Examples of various kinds of tissues; A, ciliated epithelium; B, stratified epithelium; C, hyaline cartilage; D, striated muscle fiber; E, nonstriated muscle fiber. (From Parker and Haswell.)

them into the body, and excretory products pass through them on their way out of the body; they also contain the end organs of the sensory apparatus and protect the body from physical contact with the outside world. In man the cuticle and lining of the alimentary canal are examples of epithelium.

(2) **Supporting and Connective Tissues** (Fig. 48 C) may be encountered in almost any part of the body. Their chief functions are two in number; (1) they bind together various parts of the body, and (2) they form rigid structures capable of resisting shocks and pressures of all kinds. These tissues consist largely of non-living substances, fibers, plates, and masses produced by the cells either within the cell-wall or outside of it. The tendons which unite muscles to bones, and the bones themselves, illustrate the two kinds of tissues in this group.

(3) **Muscular tissues** (Fig. 48 D, E) are the agents of active movement. We found (Chap. IV) that the locomotion of *Ameba* could be explained by the presence of contractile fibers. In other Protozoons belonging to the Classes Infusoria and Sporozoa there are muscular fibrils called myonemes in the membranous coverings. In most of the higher organisms special muscle cells are differentiated for performing the various movements of the body. These cells possess muscle fibrils which are able to contract with great force and in quick succession. The fibrils are usually of two kinds; (*a*) cross striated (D) and (*b*) smooth non-striated (E). The latter form a less highly developed tissue than the former and are found in the simpler inactive animals, and in those internal organs of higher organisms not subject to the will of the animal.

(4) **Nervous tissue** is composed of cells which are so acted upon by external physical and chemical agents that they are able to perceive a stimulus, to conduct it to some other cell or cells of the body, and to stimulate still other cells to activity. All protoplasm is *irritable;* animals without nervous systems, *e.g. Amebæ*, are capable of reacting to a stimulus, but in more complex organisms certain cells are specialized for the sole pur-

pose of performing the functions described above as characteristic of nervous tissue.

2. The Germ Cells

We have seen that the substance of which all animals are composed may be separated into reproductive and non-reproductive. The latter is called *somatic-plasm,* the former *germ-plasm.* No organism arises fully developed, but usually originates from a union of two germ cells which have been produced by a preexisting organism. There is a gradual development of an individual from the fertilized germ cell, the organism passing through a number of well-defined stages before the adult condition is attained. To bring the various steps of this process clearly before us we shall now discuss the origin and ripening of the germ cells, their union in fertilization, and the subsequent developmental history of the zygote thus formed. These subjects will be considered in some detail for each type studied in the following chapters, so we shall here give only a general outline which will serve as a foundation for future discussions.

Early in the history of the individual certain cells are set aside for the sole purpose of reproduction; these are the *germ cells.* All the other cells of the developing organism become more or less specialized for the various vegetative functions, and may eventually be recognized as nerve cells, muscle cells, etc. Only the germ cells remain in their primitive condition, and, since they take no part in the daily life of the animal, we may think of them as being passively carried about and protected by the somatic cells. Just before the individual becomes sexually mature, the germ cells awake to activity and a number of complex processes are inaugurated which result in the casting out of certain of them by the body to produce new individuals similar to the parent organism.

Spermatogenesis. — The development of the male germ cell or spermatozoon is termed spermatogenesis. As shown in Figure 49, this process may be divided into three periods: (1) the multiplica-

tion of the primordial germ cells or spermatogonia, (2) the growth of these cells, and (3) their ripening or maturation. These stages occur in all Metazoa, from the lowest to man. No one knows how many cells are produced during the period of multiplication. The last generation of spermatogonia gives

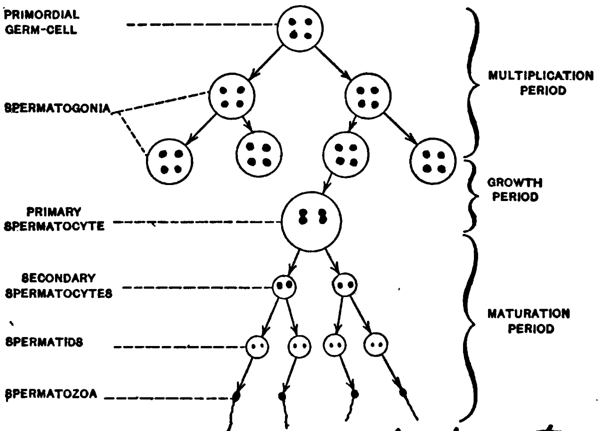


FIG. 49. Diagram illustrating the stages of spermatogenesis. The primordial germ cell is represented as possessing four chromosomes.

Maturation

rise by division to the primary spermatocytes. The latter increase greatly in size during the long growth period, and in each of them the chromosomes unite or conjugate to form *double* or *bivalent* chromosomes. Each primary spermatocyte gives rise by division to two *secondary spermatocytes*. During this division the chromosomes, which united to form the bivalent chromosomes, separate, one single or univalent chromosome going to each secondary spermatocyte. This is the only known case in cell division where entire chromosomes are separated from one another, except the corresponding stage in oogenesis. It is known as a reduction division because it results in a reduction in the number of chromosomes to one half in the daughter cells. The secondary spermatocytes immediately

divide, each forming two *spermatids*. Each spermatid receives one half of each chromosome from the secondary spermatocyte that gives rise to it. The spermatids are then metamorphosed into *spermatozoa*.

The *spermatozoa* of various animals are usually easily distinguished one from another, but are mostly constructed on the

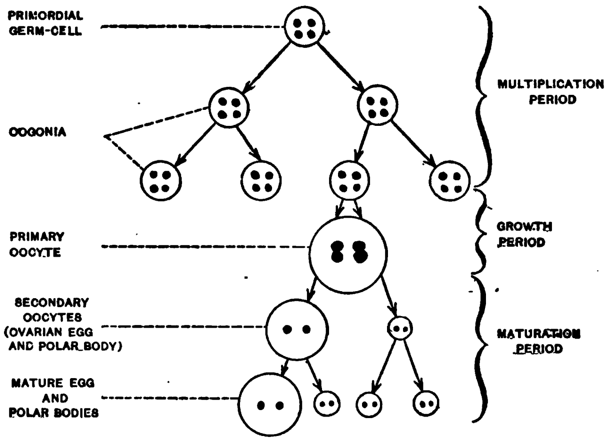


FIG. 50. Diagram illustrating the stages of oogenesis. The primordial germ cell is represented as possessing four chromosomes.

same plan. They resemble an elongated tadpole, having a head filled almost entirely with nuclear material and a long flagellum-like tail, which is the organ of locomotion; the middle piece joining these two is the centrosome. The spermatozoa are the active germ cells; it is their duty to seek out and fertilize the larger stationary egg cells. Frequently they are only $\frac{1}{100,000}$ the size of the egg, and in the sea urchin, *Toxopneustes*, their bulk is about $\frac{1}{500,000}$ the volume of the ovum (99).

Oogenesis. — The origin of the egg is called oogenesis (Fig. 50). Stages are passed through by the germ cells corresponding almost exactly to those described under spermatogenesis (Fig. 49). Before the growth period the germ cells which will produce eggs are known as *oogonia* (Fig. 50; Fig. 51, *a*). At the completion

of the growth period they are termed *primary oocytes* (Fig. 51, *b*). The primary oocytes contain only one half the number of chromosomes characteristic of the somatic cells and oogonia. As in the primary spermatocytes, these chromosomes are *bivalent,*

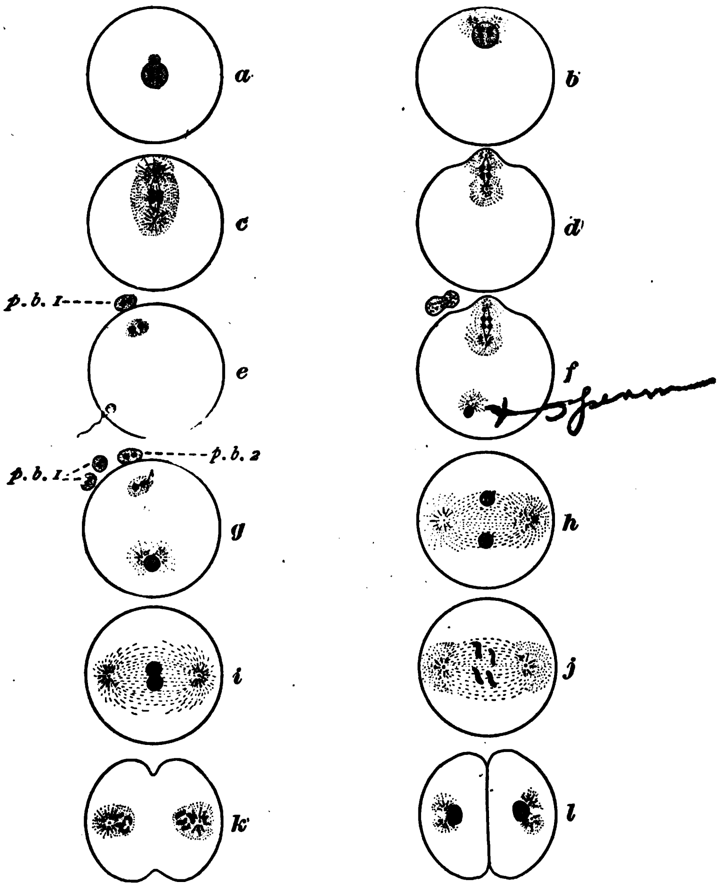


FIG. 51. Diagrams illustrating the maturation, fertilization, and cleavage of an egg. The primordial germ cell is represented as possessing four chromosomes.

resulting from the union two by two of the univalent chromosomes of the oogonia. The primary oocyte divides in the following manner. Its nucleus, called the *germinal vesicle* (Fig. 51, *a*), moves to the periphery (*b*) where a mitotic figure is formed perpendicular to the surface of the egg (*c*). A small bud-like protrusion is now formed into which pass one univalent chromosome from each of the bivalent chromosomes present in the primary oocyte (*d*). The bud is then pinched off. Two *secondary oocytes* are produced by this division, each containing an equal amount of chromatin, but one with a great deal more cytoplasm and yolk than the other (*e*). The small one is known as the *first polar body* (*e, p. b.* 1) and is not functional; the larger is the *egg*. Each secondary oocyte now prepares for division (*f*). The first polar body in some cases does not divide; when it does the division is equal (*g, p. b.* 1). The egg throws off a *second polar body* (*g, p. b.* 2) which contains one half of each chromosome. This second polar body disintegrates, as does the first.

Fertilization. — The mature ovum now becomes the center of the interesting process of fertilization. The spermatozoon sometimes enters the egg before the polar bodies are formed, and sometimes afterward. In the illustrations (Fig. 51, *f*) we have shown the sperm entering the egg at the end of the first oocyte division. The sperm brings into the egg a nucleus, a centrosome, and a very small amount of cytoplasm. The sperm nucleus soon grows larger by the absorption of material from the cytoplasm of the egg, and the centrosome begins its activity. A mitotic figure soon grows up (*g*) and moves toward the center of the egg. The egg nucleus also moves in this direction (*h*), and finally both the male and female nuclei are brought together in the midst of the spindle produced about the sperm nucleus (*i*). This completes the process usually known as fertilization. In this process the chief aim so far seems to be *the union of two nuclei, one of maternal origin, the other of paternal origin.* We shall see later that fertilization is really not consummated until the animal which develops from the egg has become sexually mature.

Chromosome Reduction. — We are able to explain now why a reduction in the number of chromosomes takes place during maturation. It has already been pointed out (p. 32) that every species of animal has a definite, even number of chromosomes in its somatic cells. This number remains constant generation after generation. Now if the mature egg contained this somatic number of chromosomes and the sperm brought into it a like number, the animal which developed from the zygote would possess in its somatic cells twice as many as its parents. The number is kept constant by reduction during the maturation divisions, so that both egg and sperm contain only one half the number in the somatic cells. The union of egg and sperm again establishes the normal number of chromosomes possessed by the parents.

Union of Chromosomes in Fertilization. — If we return for a moment to the subject of maturation, the final process in fertilization may be understood. It appears that chance has very little to do with the union of chromosomes in pairs during the early history of the germ cells (pp. 103-106, Figs. 49, 50, 51, *b*); but that one chromosome of each pair came originally from the egg and is therefore maternal, while the other was derived from the sperm and is paternal. Since the chromosomes are recognized as the bearers of hereditary qualities (p. 32) it follows that the blending of the characteristics of the mother and father in the germ cells does not occur when the sperm enters the egg, but when the individual developing from the zygote becomes sexually mature.

3. Embryology

Cleavage. — The division of the fertilized egg is known as cleavage. The chromatin of the united germ nuclei condenses into chromosomes, which are so arranged on the first cleavage spindle (Fig. 51, *j*) that each daughter nucleus receives half of each. This means that each daughter cell will contain *half of each chromosome of paternal origin and half of each chromosome of*

maternal origin. Further mitotic divisions insure a like distribution to every cell in the body. After nuclear division comes the division of the entire cells into two (*k* and *l*).

Typically the fertilized egg divides into two cells, these two into four, these four into eight, etc., each cleavage plane being perpendicular to the last preceding plane (Fig. 53). This is known as *total cleavage,* and is characteristic of *holoblastic* eggs. Other eggs are said to be *meroblastic* because they exhibit *partial cleavage,* that is, only a small part of the egg enters into cell division, the remainder serving as nutritive material for the cleavage cells. In all we can recognize four distinct types of cleavage: (1) *equal cleavage,* where the egg divides into two equal halves (Fig. 52, A); (2) *unequal cleavage,* where the first division of the egg results in one large and one small cell (Fig. 52, B); (3) *discoidal cleavage,* where the entire egg does not divide, but small cells are cut off at the surface and form a disk-shaped region (Fig. 52, C); and (4) *superficial cleavage,* where the nucleus of the egg divides rapidly; the daughter nuclei migrate to the periphery and form a single layer of cells at the surface (Fig. 52, D).

That part of ontogeny which concerns the development of an animal from the egg to maturity is known as *embryogeny.* Certain stages in this development have been recognized as common to all higher animals, and have been given names. The stages occur in a certain regular order, and as an introduction to the more detailed special accounts given for each type studied in subsequent chapters, we shall present a brief embryological history of a typical holoblastic egg. The stages to be considered are: (1) cleavage, (2) the morula, (3) the blastula, (4) the gastrula, (5) the formation of germ layers, and (6) organogeny.

Cleavage in a holoblastic egg (Fig. 53) results in the production of two (B), four (C, D), eight (E), sixteen (F), etc., cells approximately equal to one another and growing smaller as their number increases. Each of these cells is known as a *blastomere.* The blastomeres do not separate as do the daughter cells produced by the binary division of *Paramecium* (Fig. 31, *o–q*) but remain

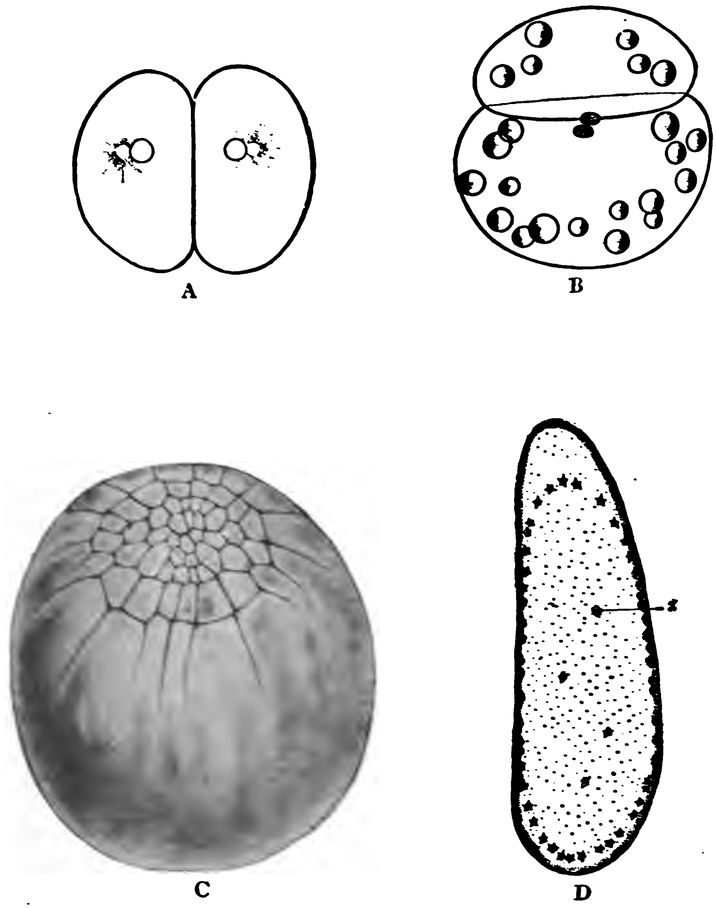


FIG. 52. Figures illustrating four different kinds of cleavage. A, equal cleavage of the sea urchin egg; B, unequal cleavage of the egg of marine worm; C, discoidal cleavage of the egg of a squid; D, superficial cleavage of an insect's egg. (A–B, from Wilson; C, from Wilson after Watasé; D, from Korschelt and Heider.)

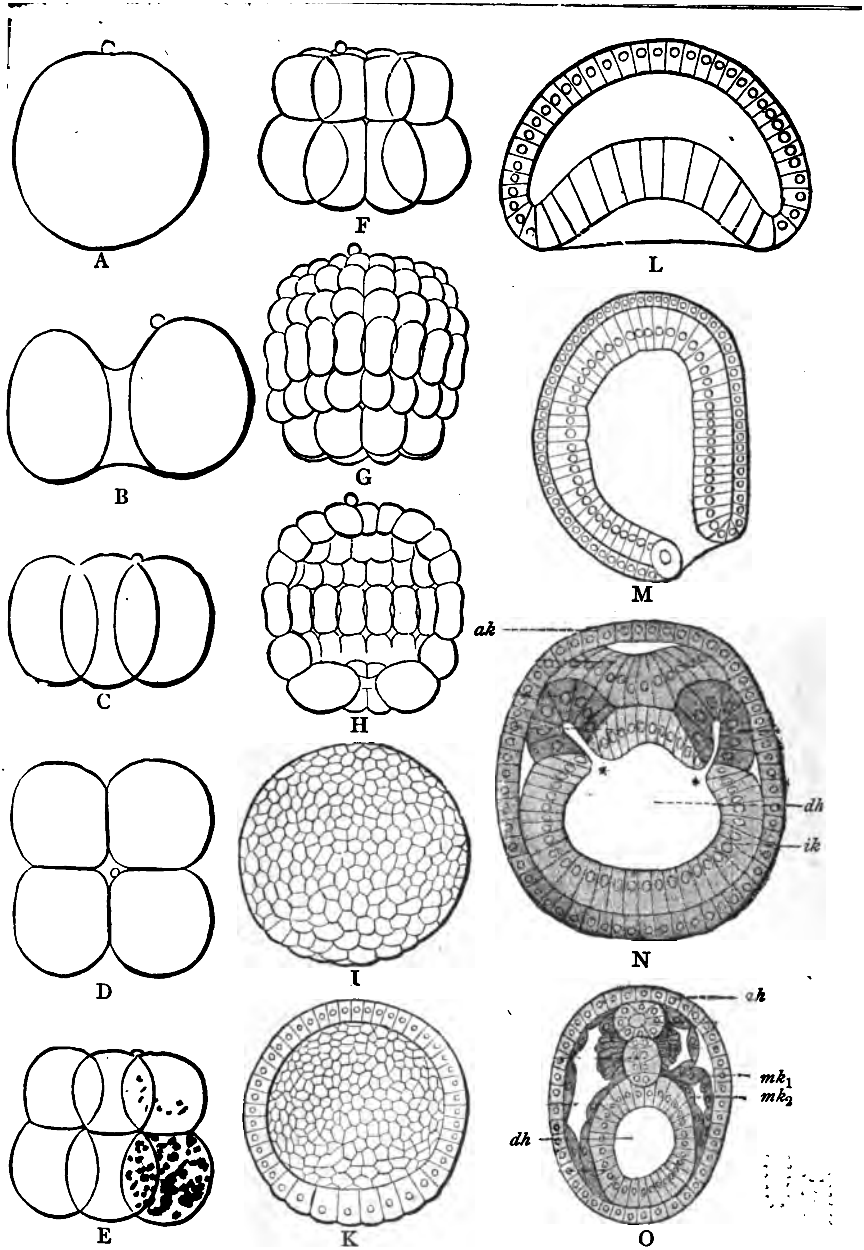


FIG. 53. Figures illustrating the cleavage of a holoblastic egg, and the formation of germ layers. A–K, cleavage and formation of the blastula; L–M, gastrulation; N, production of the mesoderm and cœlomic cavities; *O*, cœlom further developed; *ak*, ectoderm; *dh*, primitive alimentary canal; *ik*, entoderm; mk_1, somatic layer of mesoderm; mk_2, splanchnic layer of mesoderm. (From Korschelt and Heider after Hatschek.)

attached to one another as was noted in the case of *Pandorina* (p. 94, Fig. 45, II). The resemblance of the group of blastomeres to a mulberry suggested the term *morula*, which is often used in describing the egg, during the early cleavage stages.

Blastula. — As cleavage advances, a cavity becomes noticeable in the center of the egg (Fig. 53, H), becoming larger as development proceeds until the whole resembles a hollow rubber ball, the rubber being represented by a single layer of cells. At this stage the egg is called a *blastula*, the cavity the *cleavage* or *segmentation cavity*, and the cellular layer the *blastoderm*. The blastula resembles somewhat a single colony of *Volvox* (Fig. 46, A).

Gastrula. — The cells on one side of the blastula are seen to be thicker than elsewhere (Fig. 53, K) and begin to invaginate (Fig. 53, L). This process results in a cup-shaped structure with a wall of two layers, an outer layer of small cells and an inner layer of larger cells. The embryo may now be called a *gastrula* (M), and the process by which it developed from the blastula is termed *gastrulation*. The cleavage cavity is almost obliterated during the invagination, while a new cavity, the primitive digestive tract or *archenteron*, is established.

Germ layers. — The cells of one layer of the gastrula resemble one another, but differ in appearance from the cells of the other layer. Each layer gives rise to certain definite parts of the body, and is therefore termed a *germ layer;* the outer is the *ectoderm* (Fig. 53, N, *ak.*), the inner, the *entoderm* (N, *ik.*). Animals with only these two layers are said to be *diploblastic;* but the majority of the higher animals have a third layer, which usually appears between the first two after the gastrula has been formed. This is the middle layer, or *mesoderm*. It originates either from the proliferation of a few special cells which may be recognized in the early cleavage stages, or from cells budded off from the inner surface of both the ectoderm and entoderm, or from pouches arising from the walls of the entoderm (Fig. 53, N). Animals with three germ layers are said to be *triploblastic*.

Organogeny. — Each germ layer gives rise to certain organs of the adult animal. An *organ* may be defined as an association of tissues having a definite form and special function. In any of the more complex animals eight systems of organs can be recognized: (1) digestive, (2) circulatory, (3) respiratory, (4) excretory, (5) skeletal and integumentary, (6) reproductive, (7) muscular, (8) nervous. The study of the origin of these organs from the germ layers is known as *organogeny*. The organs derived from the different germ layers may be briefly listed as follows. From the *ectoderm* arise the epidermis, epithelium of various organs, and the nervous system; from the *mesoderm* come the muscles, connective and supporting tissues and blood and blood vessels; the *entoderm* becomes the epithelium of the digestive tract, pharynx, and respiratory tract.

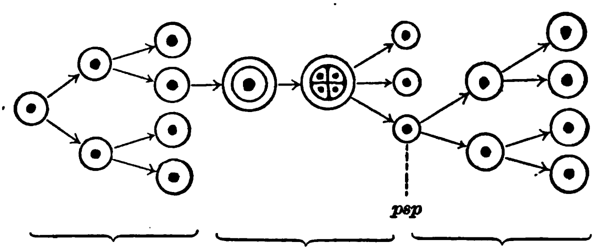
Cœlom. — Figure 53, N, O shows one method of origin of the cœlom, a cavity of great importance in the bodies of many of the complex Metazoa. Two pouches (N) formed from the inner layer of the gastrula are pinched off and come to lie one on either side of the alimentary canal (O). The cavities of these sacs constitute the cœlom. By a lateral growth and a breaking through at the ends of the sacs, the cavities unite to form a single space between the alimentary canal and the body wall. All Metazoons are frequently separated into two groups, the *cœlomata* and the *acœlomata*, according as the cœlom is present or absent. Of the types considered in the following chapters *Hydra* may be mentioned as an acœlomate, the earthworm as a cœlomate.

Table III contains a series of diagrams and descriptions which are intended to represent the methods of reproduction exhibited by the types already studied, and to show those of certain Metazoa as well. In order to make the diagrams as simple as possible certain details have beeen omitted; nevertheless, it is believed that a correct idea of the reproductive processes will be gained in every case.

TABLE III

DIAGRAMS ILLUSTRATING THE METHODS OF REPRODUCTION IN PROTOZOA AND METAZOA

A. A simple Protozoon (*Ameba*).

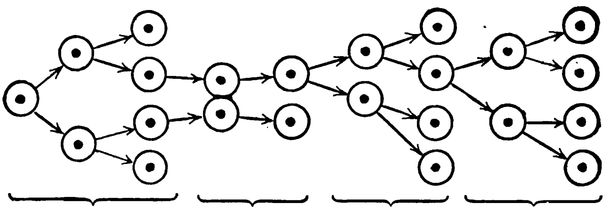


CELL DIVISION
(Binary Fission)
An indefinite number of generations.

ENCYSTMENT AND SUBSEQUENT CELL DIVISION
(Sporulation)
Many pseudopodiospores (*psp*) (young *Amebæ*) produced.

CELL DIVISION
(Binary Fission)
An indefinite number of generations.

B. A simple Protozoon (*Paramecium*).



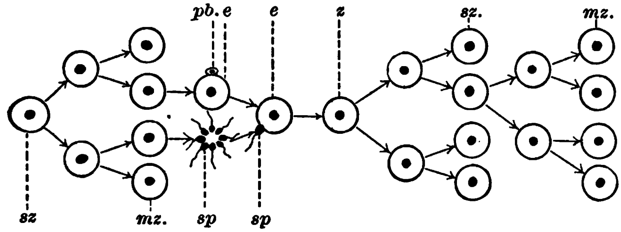
CELL DIVISION
(Binary Fission)
An indefinite number of generations.

TEMPORARY CONJUGATION
(Fertilization)
Each cell fertilizes the other.

CELL DIVISION
(Period of Reconstruction)
Each fertilized cell gives rise to four normal animals.

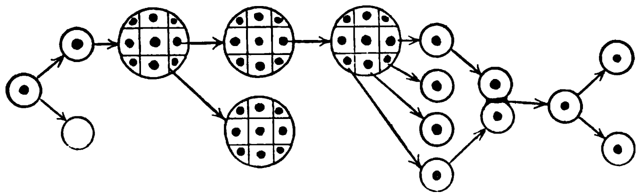
CELL DIVISION
(Binary Fission)
An indefinite number of generations.

C. A simple Protozoon (*Plasmodium*).



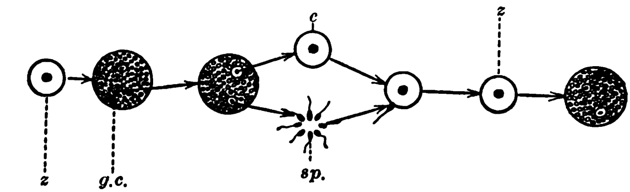
CELL DIVISION (Schizogany) A sporozoite (*sz*) produces many merozoites (*mz*).	CELL DIVISION (Gametogenesis) Certain merozoites divide, forming one egg (*e*) and one polar body (*pb*); others give rise by division to as many as eight spermatozoa (*sp*).	PERMANENT CONJUGATION (Fertilization) A female cell (*egg*) fuses with a male cell (*sperm*) producing a zygote (*z*).	CELL DIVISION (Sporogany) A zygote gives rise to many sporozoites(*sz*).	CELL DIVISION (Schizogany) A sporozoite produces many merozoites(*mz*)

D. A simple colony of cells (*Pandorina*).



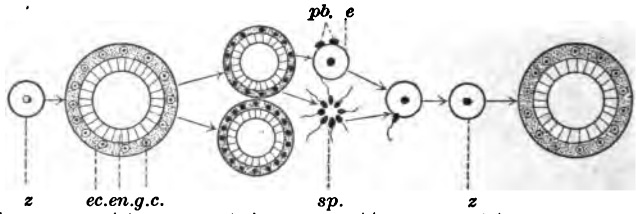
CELL DIVISION (Swarm spore formation) Zygote gives rise to from 1 to 3 swarm spores.	CELL DIVISION (Colony formation) Each swarm spore produces a new colony.	CELL DIVISION (Colony formation) Each cell of the colony produces a new colony.	CELL DIVISION (Gamete formation) Each cell of the colony produces a colony of gametes which separate from one another.	PERMANENT CONJUGATION The gametes unite in pairs, forming zygotes.	CELL DIVISION (Swarm spore formation) Zygote gives rise to 1 to 3 swarm spores.

E. A more complex colony of cells (*Volvox*).



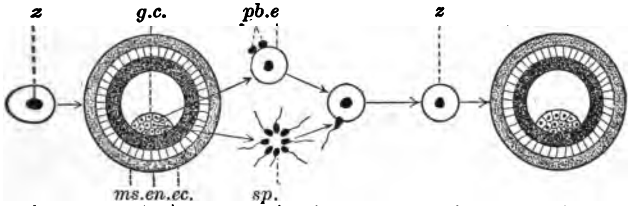
CELL DIVISION (Colony formation) Zygote (z) develops into a colony.	CELL DIVISION (Asexual Reproduction) Germ cells (*g.c.*) give rise to new colonies.	CELL DIVISION (Gamete formation) Certain germ cells produce eggs (*e*); others spermatozoa (*sp.*).	PERMANENT CONJUGATION (Fertilization) One sperm fuses with one egg, forming a zygote (z).	CELL DIVISION (Colony formation) Zygote develops into a colony.

F. A simple Metazoon (*Hydra*).



CELL DIVISION (Embryological development) Zygote (z) produces animal containing germ cells (*g.c.*) and two layers of specialized somatic cells, the ectoderm (*ec.*) and entoderm (*en.*).	BUDDING (Asexual Reproduction) Part of animal separates from parent and leads separate existence.	CELL DIVISION (Gamete formation) Certain germ cells produce one egg (*e*) and two polar bodies (*pb.*); others produce many sperms (*sp.*).	PERMANENT CONJUGATION (Fertilization) One sperm unites with one egg, forming a zygote (z).	CELL DIVISION (Embryological development) Zygote (z) produces animal, etc.

G. A complex Metazoon (*Lumbricus*).



CELL DIVISION (Embryological development)	CELL DIVISION (Gamete formation)	PERMANENT CONJUGATION (Fertilization)	CELL DIVISION (Embryological development)
Zygote (*z*) produces body containing germ cells (*g.c.*) and three layers of specialized somatic cells, the ectoderm (*ec.*), mesoderm (*ms.*), and entoderm (*en.*).	Certain germ cells produce one egg (*e*) and two polar bodies (*pb.*); others produce many sperms (*sp.*).	One sperm unites with one egg forming a zygote (*z*).	Zygote (*z*) produces body, etc.

CHAPTER VIII

HYDRA AND CŒLENTERATES IN GENERAL

1. Hydra

(*Hydra fusca* Linnæus)

Hydra fusca is a simple Metazoon abundant in fresh water ponds and streams. If a quantity of aquatic vegetation is gathered and placed in glass dishes full of water, these little fresh-water polyps will be found clinging to the plants and the sides and bottom of the dish. They are easily seen with the naked eye, being from 2 to 20 mm. in length, and may be likened to a short thick thread frazzled at the unattached, distal end. The great variation in length is due to the fact that both body and tentacles are capable of remarkable expansion and contraction because of the presence of specialized muscle fibrils in many of the cells.

TABLE IV

THE NAMES AND CHARACTERISTICS OF THE PRINCIPAL SPECIES OF HYDRA (105)

Genus	Species	Color	Tentacles	Nematocysts	Sexual Condition	Length of Body	When Sexually Mature
Hydra	*fusca*	brown	10–6 or fewer	large	Hermaphroditic	2 cm.	Sept.–Oct.
"	*viridis*	green	5–12	small	"	1–1.5 cm.	Apr.–Oct.
"	*grisea*	gray	5–18	very large	"	2 cm.	Apr.–Aug. sometimes to Dec.
"	*diœcia*	pale yellow or reddish brown	5–8		sexes distinct	2.5 cm.	Oct.–Dec.

A number of species of *Hydras* are recognized by zoologists; some of the characteristics of the principal ones are given in Table IV. *Hydra fusca* has been selected as a type because it is the species most easily obtained for laboratory use.

External Characters. — The *body* of *Hydra fusca* resembles an elastic tube which varies in length and thickness according as the animal is extended or contracted; in the former case it may reach a length of 2 cm. At the distal end is a circlet of from six to ten slender, finger-like projections called *tentacles*. The diameter of the body is frequently increased at certain points by a distention due to the ingestion of large particles of food. The general *color* is brown. Usually two regions may be noted; a thin, nearly colorless portion just below the tentacles and a thicker and more deeply colored part extending to the opposite pole. The part of the body which is usually attached to some object is known as the *foot* or *basal disk* and is referred to as the *proximal end*. The foot not only anchors the animal when at rest, but also serves as a locomotor organ. A conical elevation, the *hypostome*, occupies the distal end of the body. It is surrounded by the tentacles, and has at the top an opening, the *mouth*. This mouth is not the simple circular orifice often described, but is star-shaped, having clefts running out from the center toward each arm (104).

The *tentacles* are capable of remarkable expansion, and may stretch out from small blunt projections to very thin threads 7 cm. or more in length; in this condition they are so thin as to be barely visible even with a lens. They move independently, capturing food and bringing it into the mouth. Their number varies as shown in Table IV. Reese (116) examined six hundred specimens of *Hydra viridis* and found from four to twelve tentacles on each. These occurred in the following proportions: 54 per cent had eight; 24 per cent, seven; 15 per cent, nine; very few animals possessed a greater number than nine, and only occasionally was one found with less than seven. The number of tentacles increases with the size and age of the animal, although

unfavorable conditions and extreme age result in a decrease (116).

Frequently specimens of *Hydra* are found which possess ***buds*** in various stages of development. Several buds are often found on a single animal, and these in turn may bear buds before detach-

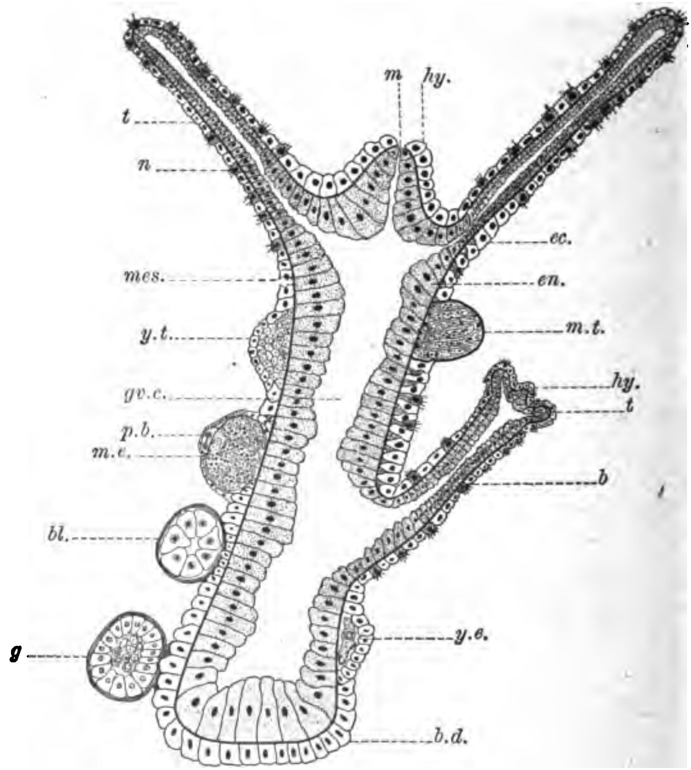


FIG. 54. Diagram of a longitudinal section of *Hydra; b.*, bud; *b.d.*, basal disk; *bl.*, blastula; *ec.*, ectoderm; *en.*, entoderm; *g.*, gastrula; *gv.c.*, gastrovascular cavity; *hy.*, hypostome; *m.*, mouth; *m.e.*, mature egg; *mes.*, mesoglea; *m.t.*, mature testis; *n.*, nematocysts; *p.b.*, polar bodies; *t.*, tentacle; *y.e.*, young egg; *y.t.*, young testis. All of the structures shown do not occur on a single animal at one time.

ment from the parent. In this way a sort of primitive *Hydra* colony is formed, resembling somewhat the asexual colonies of some of the more complex Cœlenterates to be described later (Fig. 65, A).

REPRODUCTIVE ORGANS may be observed on specimens of *Hydra fusca* in September and October. Both an *ovary* and *testes* are produced on a single individual; the former is knob-like, occupying a position about one third the length of the animal above the basal disk; the testes, usually two or more in number, are conical elevations projecting from the distal third of the body.

Structure (Fig. 54). — *Hydra* is a diploblastic animal consisting of two cellular layers, an outer thin colorless layer, the *ectoderm* (*ec.*), and an inner layer, the *entoderm* (*en.*), twice as thick as the outer and containing the brown bodies which give *Hydra fusca* its characteristic color. Both layers are composed of *epithelial cells.* A thin space containing a jelly-like substance, the *mesoglea* (*mes.*) separates ectoderm from entoderm. Not only the body wall, but also the tentacles, possess these three definite regions. The body, with the exception of the basal disk, is covered by a thin transparent *cuticle.* Both body and tentacles are hollow, the single central space being known as the *gastrovascular cavity* (*gv.c.*).

ECTODERM. — The ectoderm is primarily *protective* and *sensory,* containing structures characteristic of these functions. Slight differences in structure are observable between the ectoderm of the tentacles and that of the body wall, while the latter differs from that of the basal disk. In the ectoderm of the body wall are two principal kinds of cells, large epitheliomuscular cells, and small interstitial cells. The latter give rise to cells called cnidoblasts which form nematocysts, and to both male and female germ cells. The *epitheliomuscular cells* are shaped like inverted cones. At their inner ends are one or more comparatively long (sometimes .38 mm.) unstriped *contractile fibers* which form a thin longitudinal muscular layer. These muscle fibers explain the remarkable powers of contraction exhibited

by *Hydra* when stimulated. Near the middle of each cell, embedded in the alveolar cytoplasm, is a nucleus containing one or two nucleoli and a network of chromatin.

NEMATOCYSTS or stinging capsules (Figs. 54, *n*; 56) are present on all parts of the body of *Hydra* except the basal disk, being most numerous on the tentacles (Fig. 55, A). Each is contained in a cell known as a *cnidoblast.* These in turn are embedded in little tubercles on the surface which give the animal a rough-appearing outline. The tubercles are ectoderm cells, each of which usually possesses one or more large nematocysts surrounded by a number of a smaller variety. Three kinds of nematocysts are found in *Hydra*. The largest is .013 mm. long and .007 mm. thick; before being discharged it is pear-shaped and occupies almost the entire cell in which it lies (Fig. 56, *nem.*). Within it is a *coiled tube* (*t*) at whose base are three large and a number of small *spines*. Projeeting from the cell near the outer end of the nematocyst is a trigger-like spine, the *cnidocil* (*cnc.*). Nematocysts may be exploded by adding a little acetic acid, or better, methyl green, to the water. The tube which is coiled within them is then everted. First, the base of the tube with the spines

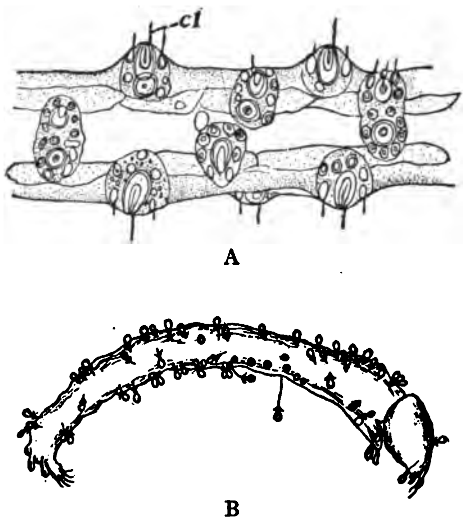


FIG. 55. Nematocysts and their action. A, portion of a tentacle showing the batteries of nematocysts; *cl.*, cnidocils; B, insect larva covered with nematocysts as a result of capture by *Hydra*. (From Jennings.)

appears, and then the rest of the tube rapidly turns inside out. Nematocysts are able to penetrate the tissues of other animals, but only at their greatest speed and before eversion is completed. Even the extremely firm chitinous covering of insects may be punctured by these structures (Figs. 55, B and 57, A). The cnidocil when touched was for a long time supposed to cause the explosion of the nematocysts, and for this reason is known as a "trigger." One can easily prove, however, that mechanical shocks have no influence upon the nematocysts. Internal pressure produced either by distortion or by osmosis, is effective. For this reason chemicals which increase the osmotic pressure within the cnidoblast cause the eversion of the thread-like tube (123, 108). An animal when "shot" by nematocysts is immediately paralyzed, and sometimes killed, by a poison called hypnotoxin which is injected into it by the tube.

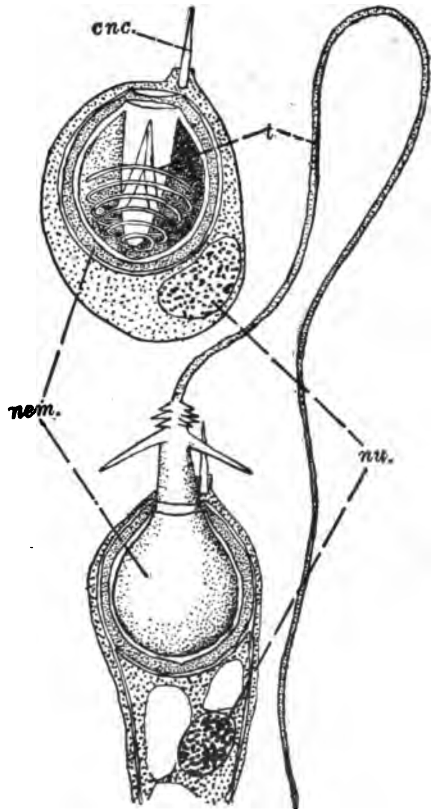
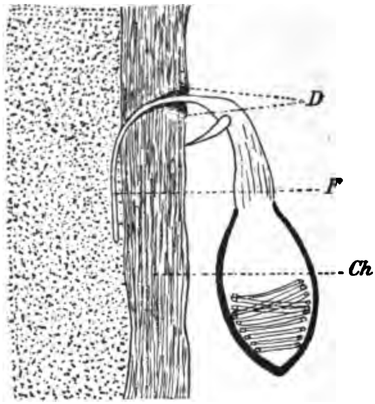


FIG. 56. Nematocysts before and after discharge. *t*, threadlike tube; *nem.*, nematocyst; *cnc.*, cnidocil; *nu.*, nucleus of cnidoblast. (From Dahlgren and Kepner after Schneider.)

Nematocysts are developed from interstitial

cells, each cell producing one nematocyst. "First a clear space appears in an interstitial cell; this space enlarges, it acquires a definite wall, and its contents stain deeply. Presently it elongates, and one end is produced to form the thread, which at its first appearance is everted and coiled round the outside of the sac. After a time the thread is introverted — it is not quite clear how — and



A

B

FIG. 57. The action of nematocysts. A, a nematocyst piercing the chitinous covering of an insect; B, nematocysts holding a small animal by coiling about its spines. (After Toppe in *Zool. Anz.*)

the nematocyst assumes its final form. When nearly ripe a nematocyst, still contained in its mother cell or cnidoblast, migrates into the inside of an epitheliomuscular cell and approaches the surface. The external end of the cnidoblast is produced to form a cnidocil which perforates the cuticle. . . ." (101, p. 259.) Since the tube of the nematocyst cannot be returned to the capsule, nor another one be developed by the cnidoblast, new capsules must be formed from interstitial cells to replace those already exploded.

The second kind of nematocyst is cylindrical (Fig. 55, A) and contains a thread which lacks the barbs so characteristic of its larger neighbor. The third variety is almost spherical and smaller than the others, measuring only .005 mm. in diameter. The thread contained in this nematocyst likewise bears no barbs, but when discharged resembles a corkscrew (Fig. 57 B). It aids in the capture of prey by coiling around the spines or other structures that may be present (121).

The interstitial cells also develop at a certain period of the year (September and October) into germ cells. The origin and history of these cells will be found fully described on pages 134–136.

The BASAL DISK (54, *b. d*) differs somewhat in function from the rest of the body. It is the point by which *Hydra* attaches itself to solid objects, and for this purpose secretes a sticky substance. It is also said to effect the movement of the animal from place to place by a sort of gliding motion, not yet fully explained, but possibly brought about by pseudopodia-like processes thrust out from some of the cells. Epitheliomuscular cells and a few interstitial cells are present, but no nematocysts are to be found here. The columnar epitheliomuscular cells are not only provided with contractile fibers at their bases, but, being secretory, also contain a large number of small refringent granules, as shown in Figure 58, *ad. sez.*

The TENTACLES (Fig. 54, *t*) are provided with an ectoderm consisting of large flat cells, thin at the edges and thick in the center. The thicker portions give the surface of the tentacle a lumpy appearance. In the center of each thickening is a

nucleus around which are embedded sometimes as many as twelve nematocysts each in its own cnidoblast (Fig. 55, A). The cnidocils projecting from the cnidoblasts resemble groups of cilia. Each cnidoblast is drawn out at its base into a contractile fibril which enters the longitudinal muscular sheet at the base of the ectoderm cells.

ENTODERM (Fig. 54, *en.*). — The inner layer of cells, the entoderm, occupies about two thirds of the body wall. Its functions are *digestive* and *secretory*. The digestive cells are long and club-shaped, with transverse muscular fibrils at their base, forming a circular sheet of contractile substance. At the larger end, which extends into the central gastrovascular cavity, are two *flagella*. *Pseudopodia* may also be thrust out from this free end. The internal structure of these cells differs before and after the animal is fed. In a starving *Hydra* large vacuoles appear, almost completely filling the cell, the protoplasm being reduced to a thin layer near the cell wall; after a meal, however, the cells are gorged with nutritive spheres, many of which, especially the oil globules, migrate into the ectoderm and are stored near the periphery, giving the animal its brown color (104).

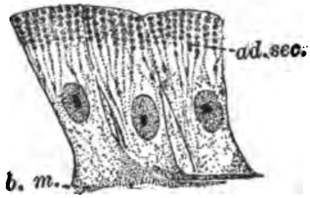


FIG. 58. Three glandular cells from the basal disk of *Hydra*. *ad. sec.*, granules of adhesive secretion. (From Dahlgren and Kepner.)

The *glandular cells* are smaller than the digestive cells, and lack the contractile fibrils at their base. They are broad at the free end, and thin out to a fine filament which ends in a knoblike enlargement when the mesoglea is reached. The gland cells also differ in appearance according to their metabolic activity: some are filled with large vacuoles containing secretory matter, while others, having discharged their secretum, appear crowded with fine granules. Interstitial cells are found lying at the base of the other entoderm cells.

The tentacle contains entoderm cells apparently devoid of muscular fibers. Gland cells are also absent from this region. The entoderm of the basal disk is provided with only a few glandular cells.

MESOGLEA (Fig. 54, *mes.*). — The mesoglea in *Hydra* is so thin as to be difficult to find, even when highly magnified; in some of the other Cœlenterates this layer is very thick, constituting by far the largest part of the body.

NERVOUS SYSTEM. — From recent investigations it seems well established that *Hydra* possesses a nervous system, though complicated staining methods are necessary to make it visible. In the ectoderm there is a sort of plexus of nerve cells connected by nerve fibers with centers in the region of the mouth and foot. Sensory cells in the surface layer of cells serve as external organs of stimulation, and are in direct continuity with fibers from the nerve cells. Some of the nerve cells send processes to the muscle fibers of the epitheliomuscular cells, and are therefore motor in function. No processes from the nerve cells to the nematocysts have yet been discovered, though they probably occur. The entoderm of the body also contains nerve cells, but not so many as are present in the ectoderm (109).

Nutrition. — FOOD. — The food of *Hydra* consists principally of small animals that live in the water. Of these may be mentioned small crustacea such as *Cyclops*, Annelids, and insect larvæ. *Hydra* normally rests with its basal disk attached to some object and its body and tentacles extended out into the water. In this position it occupies a considerable amount of hunting territory. Any small aquatic animal swimming in touch with a tentacle is at once shot full of nematocysts (Fig. 55, B), which not only seem to paralyze it, but also to hold it firmly. There is some evidence to prove that the tentacles are able to secrete a fluid which serves to paralyze the animal without the aid of nematocysts (123). The viscid surface of the tentacle aids in making sure that the victim does not escape.

INGESTION. — Ingestion takes place as follows: First, the

tentacle, which has captured the prey, bends toward the mouth with its load of food. The other tentacles not only assist in this, but may use their nematocysts in quieting the victim. The mouth often begins to open before the food has reached it. The edges of the mouth gradually inclose the organism and force it into the gastrovascular cavity. The body wall contracts behind the food and forces it down until it reaches the basal end of the body. Here it remains during the process of digestion. Frequently organisms many times the size of the *Hydra* are successfully ingested.

Reactions to Food.—It is not uncommon to find *Hydras* that will not react to food when it is presented to them. This is due to the fact that these animals will eat only when a certain interval of time has elapsed since their last meal. The physiological condition of *Hydra*, therefore, determines its response to the food stimulus. The collision of an aquatic organism with the tentacle of *Hydra* is not sufficient to cause the food-taking reaction, since it has been found that not only a mechanical stimulus, but also a chemical stimulus must be present. A very hungry *Hydra* will even go through the characteristic movements when it is excited by the chemical stimulus alone. This has been shown by the following experiment. When the tentacles and hypostome of a moderately hungry *Hydra* are brought into contact with a piece of filter paper, which has been soaked for a time in the same culture medium, there is no response. If the filter paper is then soaked in beef juice and offered to the *Hydra*, the usual food reactions are given.

Beef juice alone calls forth no response in a moderately hungry animal; but does inaugurate the normal reflex, if a very hungry specimen is selected for the experiment. The conclusion reached is that well-fed *Hydras* will not respond to either mechanical or chemical stimuli when acting alone or in combination; that moderately hungry animals will react to a combination of the two, and that hungry animals will exhibit food-taking movements even if a chemical stimulus alone is employed (123).

DIGESTION.—Immediately after the ingestion of food the gland cells in the entoderm show signs of great activity; their nuclei enlarge and become granular. This is due probably to the formation of enzymes which are discharged into the gastrovascular cavity and begin at once the dissolution of the food. The action of the digestive juices is made more effective by the churning of the food as the animal expands and contracts. The cilia extending out into the central cavity also aid in the dissolution of the food by creating currents. This method of digestion differs from that of *Ameba* and *Paramecium* in being carried on outside of the cell; *i.e.* extracellular. There is evidence that intracellular digestion also takes place in *Hydra;* the pseudopodia thrust out by the entoderm cells seize and engulf particles of food which are dissolved within the cells. However, most of the food is digested in the gastrovascular cavity. The digested food is absorbed by the entoderm cells; part of it, especially the oil globules, is passed over to the ectoderm, where it is stored.

EGESTION. — All insoluble material is egested from the mouth. This is accomplished by "a very sudden squirt" which throws the débris to some distance (123).

Behavior. — *Hydra viridis* gives a more prompt and decisive response when stimulated than any other species of *Hydra,* and for this reason its behavior has been studied more thoroughly than that of the others. The following paragraphs have been compiled largely from experiments upon green *Hydras,* although enough work has been done with other forms to prove that their reactions are practically the same, only more sluggish.

NORMAL POSITION OF HYDRA. —*Hydras* may be found attached to the sides or bottom of an aquarium, to parts of water plants, or hanging from the surface film. Usually they are near the top where more oxygen can be obtained from the water than at greater depths. If attached to the bottom, the body is usually held upright; if to the sides, the body is in most cases horizontal, the hypostome generally being lower than the foot; and if to the surface film, the body is allowed to hang directly downward.

Suspension from the surface film may be compared with that of a needle placed on the surface of the water (122). Threads of a gelatinous substance, extending out from the basal disk, help sustain the body, while in some cases a large air bubble attached to the foot keeps the animal afloat (123). The position of rest in every case gives the *Hydra* the greatest opportunities for capturing food, since in this condition it has control of a large amount of territory.

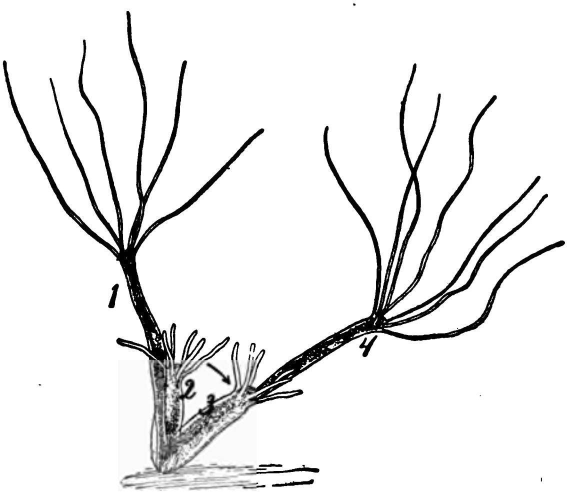


FIG. 59. Spontaneous changes of positions in an undisturbed *Hydra*. Side view. The extended animal (1), contracts (2), bends to a new position (3), and then extends (4). (From Jennings.)

SPONTANEOUS MOVEMENTS. — All the movements of *Hydra* are the result of the expansion or contraction of the muscle fibers, and are produced by two kinds of stimuli, internal, or spontaneous, and external. Spontaneous movements may be observed when the animal is attached and undisturbed. At intervals of several minutes the body, or tentacles, or both, contract suddenly and rapidly, and then slowly expand in a new direction. Hungry specimens are more active than well-fed individuals. The result

is to bring the animal into a new part of its surroundings, where more food may be present (Fig. 59). These movements finally cease, and the animal's position is changed by locomotion.

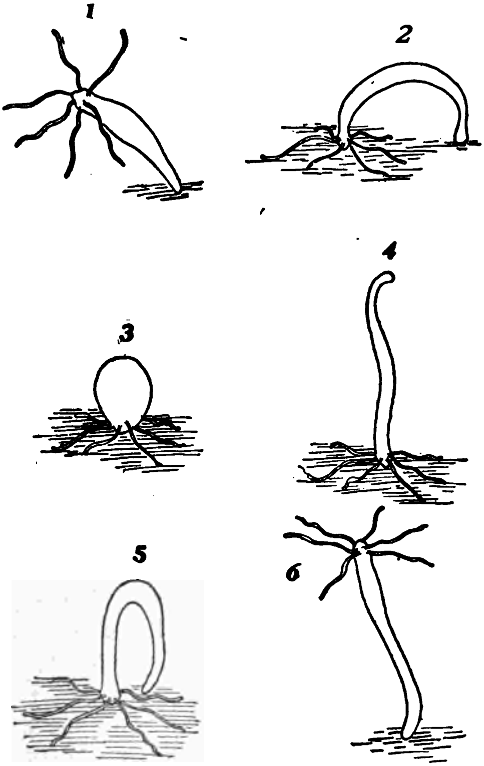


FIG. 60. *Hydra* moving like a measuring worm. (From Jennings after Wagner.)

LOCOMOTION. — Movement from place to place is effected in one of three ways. In most cases the animal bends over (Fig. 60, 1) and attaches itself to the substratum by its tentacles (2), probably with the aid of pseudopodia thrust out by the ectoderm cells. The basal disk is then released and the animal con-

tracts (Fig. 60, 3). It then expands (4), bends over in some other direction and attaches its foot (5). The tentacles now loosen their hold and an upright position is regained (6). The whole process has been likened to the looping locomotion of a measuring worm. At other times the animal moves from place to place while inverted by using its tentacles as legs. Locomotion may also result from the gliding of the foot along the substratum, and considerable distances are sometimes covered in this way.

REACTIONS TO EXTERNAL STIMULI. — THIGMOTROPISM. — *Hydra* reacts to various kinds of special stimuli. Reaction to contact accounts for its temporary fixed condition. The attachment while in the resting attitude is a result of this reaction, and not a response to gravity, since *Hydras* have the longitudinal axis of the body directed at every possible angle regardless of the force of gravity. Mechanical shocks, such as the jarring of the watch glass containing a specimen, or the agitation of the surface of the water, cause a rapid contraction of a part or all of the animal. This is followed by a gradual expansion until the original condition is regained.

Mechanical stimuli may be *localized* or *non-localized*. That just noted is of the latter type. *Local stimulation* may be accomplished by touching the body or tentacles with the end of a fine glass rod. The reactions to local stimuli variously applied have been classified as follows: —

"A. Stimulation of body:
- 1. Weak: body partly contracts.
- 2. Medium: body completely contracts.
- 3. Strong: body and tentacles contract.

B. Stimulation of a tentacle:
- 1. Weak: tentacle stimulated contracts.
- 2. Medium: all tentacles contract.
- 3. Strong: tentacles and body contract" (123, p. 594).

It should be noted that the stimulation of one tentacle may cause the contraction of all the tentacles (B, 2), or even the contrac-

tion of both tentacles and body (B, 3). This shows that there must be some sort of transmission of stimuli from one tentacle to another and to the body. The structure of the nervous system would make this possible (see p. 125)

PHOTOTROPISM. — There is no definite response to light, although the final result is quite decisive. If a dish containing *Hydras* is placed so that the illumination is unequal on different sides, the animals will collect in the brightest region, unless the light is too strong, in which case they will congregate in a place where the light is less intense. *Hydra* therefore has an optimum with regard to light. The movement into or out of a certain area is accomplished by a method of "trial and error." When put in a dark place *Hydra* becomes restless and moves about in no definite direction; but if white light is encountered, its locomotion becomes less rapid and finally ceases altogether. The value to the organism of such a reaction is quite important, since the small animals that serve as food for it are attracted to well-lighted areas. *Colored lights* have the same effect as darkness; blue, however, is preferred by *Hydra* to white.

THERMOTROPISM. — The reactions of *Hydra* to changes in temperature are also indefinite, although in many cases they enable the animal to escape from a heated region. No locomotory change is produced by temperatures below 31° C.; at this temperature, however, the basal disk is released and the animal takes up a new position either away from the heated area or further into it. In the former case the *Hydra* escapes, in the latter it may escape if subsequent movements take it away from the injurious heat, otherwise it perishes. *Hydra* does not move from place to place if the temperature is lowered; it contracts less rapidly, and finally ceases all its movements when the freezing point is approached (113).

ELECTROTROPISM. — An attached *Hydra*, when subjected to a weak constant electric current, bends toward the anode, its body finally becoming oriented with the basal disk toward the cathode and the anterior end toward the anode side. The entire animal

then contracts. In an animal attached by the tentacles a similar bending occurs, but the basal disk in this case is directed toward the anode. These reactions are caused by local contractions on the anode side for which the electric current is directly responsible (115).

Hydra shows no *rheotropic reactions.* When placed in a current of water it neither orients itself in a definite way nor moves either up or down stream (123).

General Remarks on the Behavior of Hydra. — It is evident from the above outline of the reactions of *Hydra* to stimuli that the only movements involved are produced by contraction and expansion of the body when attached, and by undirected changes of position. Being radially symmetrical, the body may be flexed in any direction.

Local stimuli, such as the application of heat or a chemical to a limited area of the body, causes a contraction of the part affected and a bending in that direction. This results in the movement of the tentacular region toward the stimuli, and the contraction of the entire animal follows, thus carrying it out of the influence of the stimulus.

Non-localized stimuli, such as the jarring of the vessel containing the animals, produces, immediately, a contraction of the entire body, which, in most cases, is beneficial, since it removes it from an injurious agent. If, however, this simple contraction is not effective, as in the case of a constant application of heat, the *Hydra* usually resorts to some other reaction, *e.g.* locomotion, which often enables it to escape from the injurious stimulus.

Finally, it should be remembered that the physiological condition of the animal determines to a large extent the kind of reactions produced, not only spontaneously, but also by external stimuli. "It decides whether *Hydra* shall creep upward to the surface and toward the light, or shall sink to the bottom; how it shall react to chemicals and to solid objects; whether it shall remain quiet in a certain position, or shall reverse this position and undertake a laborious tour of exploration" (110, p. 231).

Reproduction. — Reproduction takes place in *Hydra* both *asexually* and *sexually;* in the former case, by fission and budding, in the latter, by the production of a fertilized egg.

LONGITUDINAL FISSION. — Since the work of Trembley (1744) appeared, a number of zoologists have reported the discovery of *double Hydras.* These were considered by some as abnormalities, and by others as undergoing the process of longitudinal fission. There seems now to be plenty of evidence to prove that *Hydra* does reproduce by longitudinal division (112). The distal end of the animal divides first; then the body slowly splits down the center, the halves finally separating when the basal disk is severed

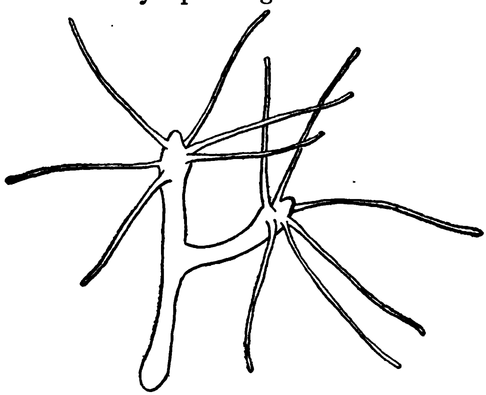


FIG. 61. *Hydra* reproducing by longitudinal division. (After Koelitz in *Zool. Anz.*)

(Fig. 61). *Hydras* have also been found which bore buds reproducing in this manner. This method of multiplication must, however, be rare since it is so seldom seen. *Transverse fission* has also been reported (111).

BUDDING (Fig. 54, *b*). — A commoner method of asexual reproduction, and one that is easily observed in the laboratory, is by budding. Superficially the bud appears first as a slight bulge in the body wall. This pushes out rapidly into a stalk which soon develops a circlet of blunt tentacles about its distal end. The cavities of both stalk and tentacles are at all times directly

connected with that of the parent. When full grown, the bud becomes detached and leads a separate existence. The details of the process are briefly as follows. The interstitial cells in a certain region increase in number and volume, producing a slight outbulging of the ectoderm. The growing region is located at the point where the edges of the protrusion meet the body wall. Here the cells are well fed and multiply actively. The ectoderm and entoderm cells of the parent give rise to the corresponding cells of the bud. When the bud is fully grown, the ectoderm cells at its proximal end secrete a sticky substance which is used later for its attachment. The entoderm cells in the same region then unite, separating the cavity of the bud from that of the parent. Finally, the bud becomes detached. The food supply determines the rate of growth of the bud, and a bud may be entirely absorbed by a starving animal (120).

Sexual Reproduction. — Whether or not there are definite germ cells in the adult *Hydra* is still open to question. So far as is known, both ova and spermatozoa arise from indifferent interstitial cells.

Spermatogenesis. — The male cells of *Hydra* are formed in little conical elevations called *testes* which project from the surface of the body (Fig. 54, *y. t.*, *m. t.*). The testis arises within the ectoderm from interstitial cells. A single interstitial cell divides mitotically; then adjacent interstitial cells also divide, multiplication continuing until the ectoderm becomes distended. An indefinite number of long multinucleated cysts (Fig. 62, A) are formed within the testis, each cyst being the product of a single or several interstitial cells. Each interstitial cell is a primordial germ cell; it gives rise by mitosis to a variable number of spermatogonia, which contain the somatic number of chromosomes, twelve. Reduction in the number of chromosomes to six occurs just after the spermatogonia have divided to form the primary spermatocytes (Fig. 62, A, *b*). The latter give rise to secondary spermatocytes (*c*) which divide at once, producing spermatids (*c*). These two spermatocyte divisions take place without the

formation of cell walls, *i.e.* each primary spermatocyte develops into a four-nucleated cell which represents the four spermatids. Within this cell the spermatids transform into spermatozoa (Fig. 62, B). A single cyst may contain representatives of all of these cell generations — spermatogonia, primary spermatocytes, secondary spermatocytes, spermatids, and spermatozoa. The mature spermatozoa break out of the vesicle in which they are formed, and swim about in the distal end of the cyst (Fig. 62, A, *d*); they finally reach the outside by way of a minute temporary opening in the end of the cyst. The mature spermatozoa swim about in the water searching for an egg; their activity continues from one to three days.

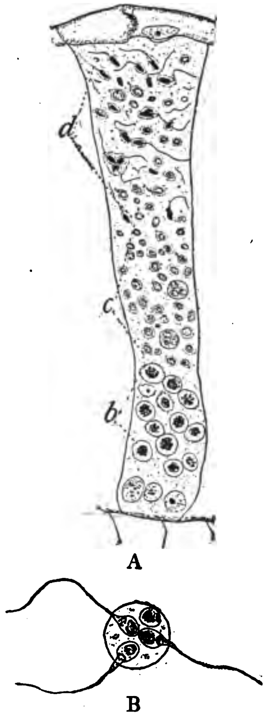
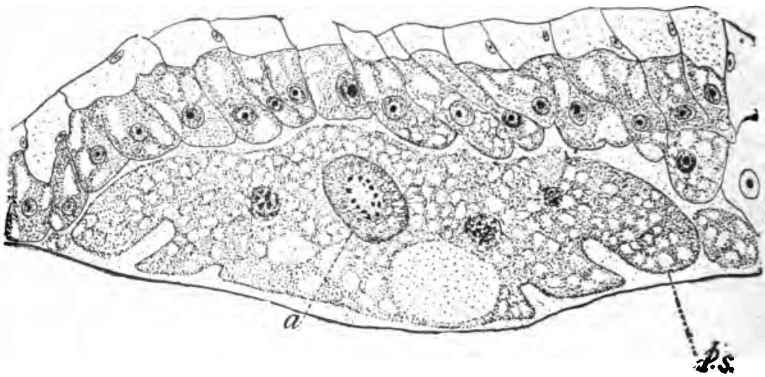


FIG. 62. Parts of a testis of *Hydra*. A, a single cyst showing spermatogonia, primary spermatocytes (*b*), secondary spermatocytes and spermatids (*c*), and spermatozoa (*d*); B, developing spermatozoa. (After Tannreuther in Biol. Bul.)

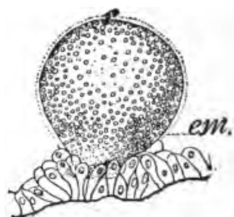
OOGENESIS. — The egg is first distinguished from the interstitial cells of the ectoderm by its slightly greater size, its spherical shape, and the comparatively large volume of its nucleus. As the eggs grow in size the neighboring interstitial cells increase in number by mitosis, and also become larger. The whole structure may at this time be called an ovary (Figs. 63, A; 54, *y. e.*). The nourishment of the egg is at first similar to that of the other ectoderm cells, but later the interstitial cells near it are engulfed, their contents becoming part of the ovum. The nuclei of these interstitial cells furnish the yolk of the growing egg. Usually only one egg is developed in a single ovary, but some-

times two may arise and complete their development side by side. In most cases, however, when two or more eggs are contained in one ovary, their adjacent walls dissolve and one of the nuclei survives while the others disintegrate. As the ovum grows it becomes



A

FIG. 63. An ovary (A), and mature egg (B) of *Hydra*. *a*, egg nucleus; *ps.*, pseudopodium of young egg; *em*, egg membrane. (After Tannreuther in Biol. Bul.)



B

ameboid in shape, showing distinct pseudopodia (Fig. 63, A, *p.s.*); these are drawn in when it has reached its full size. The egg is now nearly spherical, and is surrounded by a single layer of ectoderm cells (Fig. 54, *m.e.*). Maturation then takes place. Two polar bodies (*p.b.*) are formed, the first being larger than the second. During maturation the number of chromosomes is reduced from the somatic number, twelve, to six. This occurs at the end of the growth period. Now an opening appears in the ectoderm and the egg is forced out, finally becoming free on all sides except where attached to the animal (Fig. 63, B).

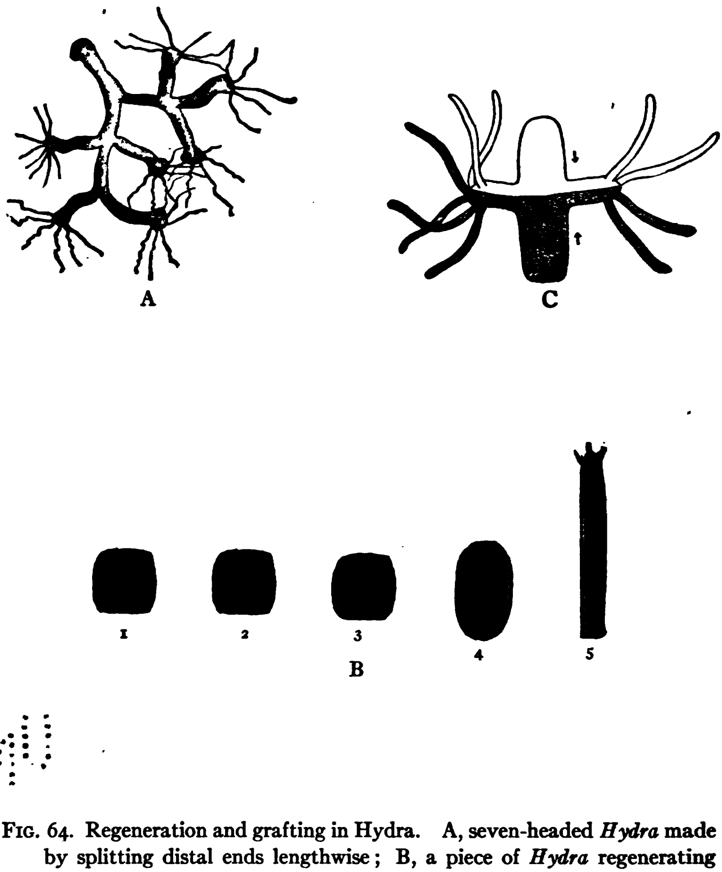


FIG. 64. Regeneration and grafting in Hydra. A, seven-headed *Hydra* made by splitting distal ends lengthwise; B, a piece of *Hydra* regenerating an entire animal; 1–5, stages in this process; C, part of one *Hydra* grafted upon another. (From Morgan, A after Trembley, B after Morgan, C after King.)

Fertilization.— Fertilization usually occurs within two hours. Several sperms penetrate the egg membrane, but only one enters the egg itself. If not fertilized within twenty-four hours, the egg becomes sterile. The sperm brings a nucleus containing six chromosomes into the egg. The male and female nuclei unite, forming the fusion nucleus.

Embryology. — *Cleavage*, which now begins, is total and regular. A well-defined cleavage cavity is present at the end of the third cleavage, *i.e.* the eight-celled stage. When the *blastula* is completed, it resembles a hollow sphere with a single layer of epithelial cells composing its wall. These cells may be called the primitive ectoderm. By mitotic division they form entoderm cells which drop into the cleavage cavity, completely filling it. The *gastrula*, therefore, is a solid sphere of cells differentiated into a single outer layer, the ectoderm and an irregular central mass, the entoderm. The ectoderm surrounds the gastrula with two envelopes. The outer is a thick chitinous shell covered with sharp projections; the inner is a thin gelatinous membrane.

Hatching. — The embryo in this condition separates from the parent and falls to the bottom, where it remains unchanged for several weeks. Then interstitial cells make their appearance. A subsequent resting period is followed by the breaking away of the outer chitinous envelope and the elongation of the escaped embryo. Mesoglea is now secreted by the ectoderm and entoderm cells; a circlet of tentacles arises at one end and a mouth appears in their midst. The young *Hydra* thus formed soon grows into the adult condition.

Regeneration. — An account of the phenomenon of regeneration is appropriate at this place, since the power of animals to restore lost parts was first discovered in *Hydra* by Trembley in 1740. This investigator found that if *Hydras* were cut into two, three, or four pieces, each part would grow into an entire animal. Other experimental results obtained by Trembley are that the hypostome together with the tentacles, if cut off, produce a new individual; that each piece of a Hydra split longitudinally

into two or four parts, becomes a perfect polyp (Fig. 64, A), that when the head end is split in two and the parts separated slightly a two-headed animal results; and that a specimen when turned inside out is able to readjust itself to new conditions forced upon it.

Regeneration may be defined as the replacing of an entire organism by a part of the same. It takes place not only in *Hydra*, but in many other Cœlenterates, and in some of the representatives of almost every phylum of the animal kingdom. *Hydra*, however, is the species that has been most widely used for experimentation. Pieces of *Hydra* that measure $\frac{1}{6}$ mm. or more in diameter are capable of becoming entire animals (Fig. 64, B). The tissues in some cases restore the lost parts by a multiplication of their cells; in other cases, they are worked over directly into a new but smaller individual.

Grafting. — Parts of one *Hydra* may easily be grafted upon another (Fig. 64, C). In this way many bizarre effects have been produced. Parts of two *Hydras* of two species have also been successfully united.

General Remarks on Regeneration. — Space will not permit a detailed account of the many interesting questions involved in the phenomena of regeneration, but enough has been given to indicate the nature of the process. The benefit to the animal of the ability to regenerate lost parts is obvious to all. Such an animal, in many cases, will succeed in the struggle for existence under adverse conditions. The regeneration of the earthworm and the crayfish are considered in Chapters X and XI. It will suffice here, therefore, to say a few words concerning regeneration in general. Regeneration takes place continually in all animals; for example, new cells are produced in the epidermis of man to take the place of those that are no longer able to perform their proper functions. Both internal and external factors have an influence upon the rate of regeneration and upon the character of the new part. Temperature, food, light, gravity, and contact are some of the external factors. In man, various tissues are

capable of regeneration; for example, the skin, muscles, nerves, blood vessels, and bones. Lost parts are not restored in man, because the growing tissues do not coordinate properly. Many theories have been advanced to explain regenerative processes, but none has gained sufficient acceptance to warrant its inclusion here.

2. Cœlenterates in General

The Characteristics and Classification of Cœlenterates. — The Phylum Cœlenterata includes the polyps, jellyfishes, sea anemones, and corals. All of these animals have a body wall consisting of two layers of cells, between which is a non-cellular substance, the mesoglea. Within the body is a single gastrovascular cavity, or cœlenteron. Because of the presence of two cellular layers, all Cœlenterates are said to be diploblastic. They are also acœlomates, *i.e.* they do not possess a second body cavity, the cœlom. All Cœlenterates are provided with nematocysts.

This phylum contains three classes, as follows: —

Class 1, Hydrozoa. This class includes the fresh-water polyps, the small jellyfishes, the hydroid zoophytes, and a few stony corals.

Class 2, Scyphozoa. Most of the large jellyfishes are placed in this class.

Class 3, Anthozoa. In this class are found the sea anemones, and most of the stony and horny corals.

Hydra is a member of the class Hydrozoa. It may be considered as a type of what is known as a *zooid*, or *polyp*. Many of the Hydrozoa living in salt water are colonial, consisting of a large number of zooids which are united so as to resemble a branching tree, *e.g.* *Obelia* (Fig. 65, A). If the buds of a *Hydra* should remain attached to their parent, and should in turn produce buds a hydroid colony somewhat like *Obelia* would result. All Hydrozoa are not fixed, but some of them swim about freely through the water. The jellyfishes, or *medusæ* (Fig. 65, B), are of this type. They are cup-shaped animals with a circlet of tentacles extending

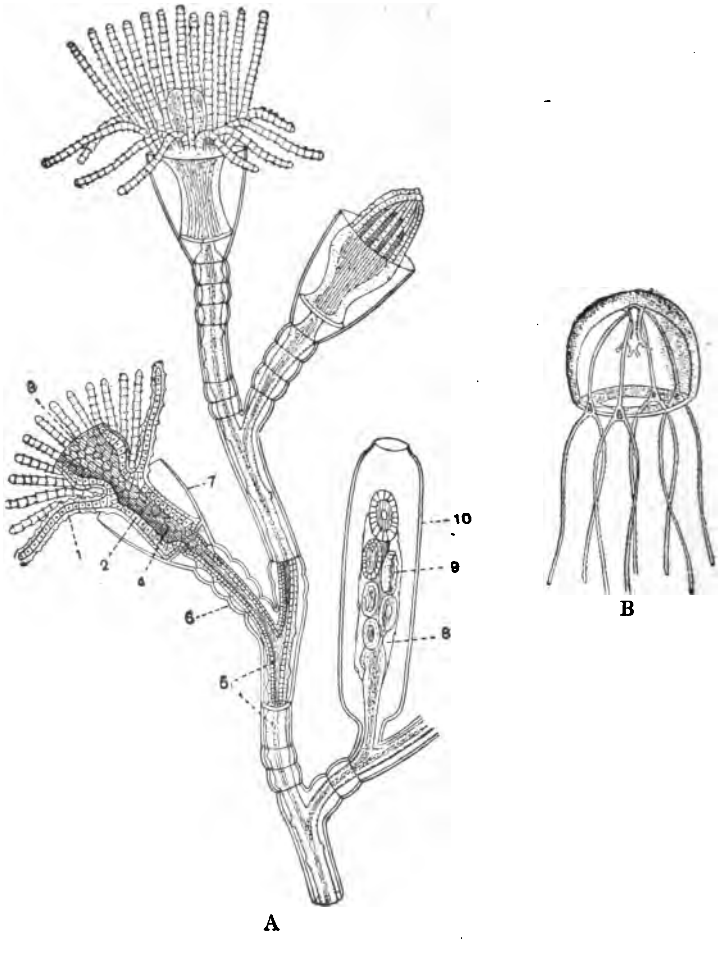


FIG. 65. Part of a colonial Hydrozoan, *Obelia* (A), and a free-swimming medusa (B) from another hydroid colony (*Bougainvillia*). 1, ectoderm; 2, entoderm; 3, mouth; 4, cœlenteron; 5, cœnosarc; 6, perisarc; 7, hydrotheca; 8, blastostyle; 9, medusa bud; 10, gonotheca. (From Shipley and MacBride.)

from the extreme rim. The middle layer, the mesoglea, is in them remarkably thick, and resembles jelly, hence their name.

Hydra and Jellyfishes Compared. — Although the medusæ upon superficial examination appear to be very different from the polyps or zooids, they are constructed on the same general

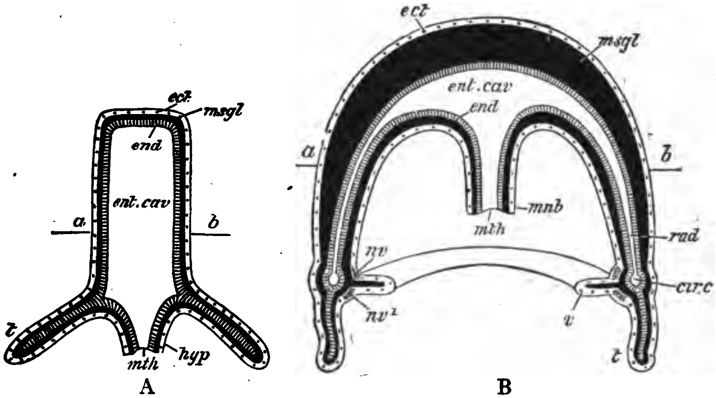


FIG. 66. Diagrams showing the similarities of a polyp (A) and a medusa (B). *circ.*, circular canal; *ect.*, ectoderm; *end.*, entoderm; *ent. cav.*, gastro-vascular cavity; *hyp.*, hypostome; *mnb.*, manubrium; *msgl.*, mesoglea; *mth.*, mouth; *nv.*, nerve rings; *rad.*, radial canal; *v.*, velum. (From Parker and Haswell.)

plan as the latter. Figure 66 illustrates in a diagrammatic fashion the resemblances between the polyp (A), and the medusa (B) by means of longitudinal sections. If the medusa were grasped at the center of the aboral surface and elongated, a hydra-like form would result. Both have similar parts, the most noticeable difference being the enormous quantity of mesoglea present in the medusa.

Metagenesis. — In some Hydrozoa there are two kinds of individuals belonging to the same species; one of these, in the form of a polyp, gives rise asexually by budding to the second form, the medusa, which produces eggs and sperms. The fertilized egg develops into the polyp. The polyp, or hydroid stage,

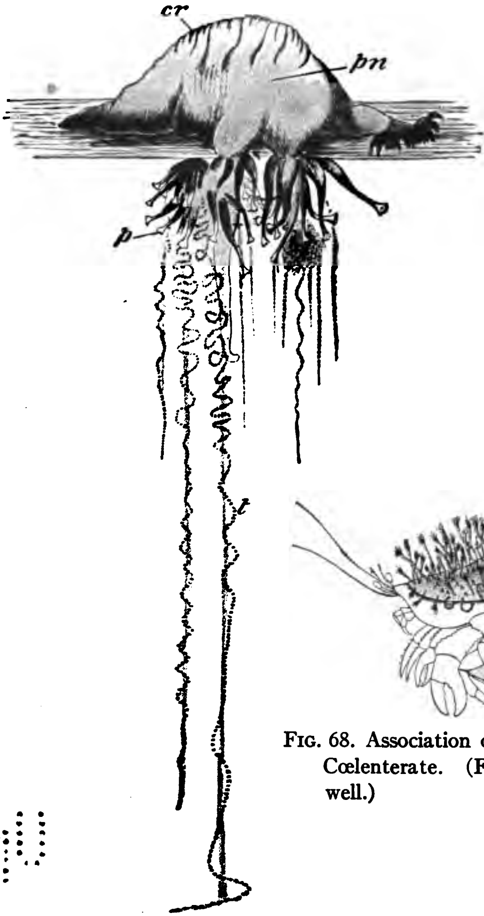
is more pronounced in some species than in others, *e.g.*, *Hydra* has no medusa stage at all; whereas certain species have no polyp stage but pass their entire existence as medusæ. Various conditions may be illustrated by different Hydrozoa. In the following table, O represents the fertilized ovum; H, a polyp; M, a medusa; m, an inconspicuous or degenerate medusa, and h, an inconspicuous or degenerate polyp (103).

1. O — H — O — H — O (*Hydra*).
2. O — H — m — O — H — m — O (*Sertularia*).
3. O — H — M — O — H — M — O (*Obelia*).
4. O — h — M — O — h — M — O (*Liriope*).
5. O — M — O — M — O (*Geryonia*).

The alternation of a sexual with an asexual generation, as in examples 2, 3, and 4, just listed, is known as *metagenesis*. This phenomenon occurs in other groups of the animal kingdom, but finds its best examples among the Cœlenterates.

Division of Labor among Cœlenterates. — Not only have the somatic cells of the Cœlenterates become differentiated into ectoderm and entoderm, in each of which cells may be recognized having particular functions to perform; but in certain groups colonial species are found in which the various members of the colony are so specialized for certain kinds of work, that they are incapable of carrying on other processes. Perhaps the best example of such a condition is *Physalia*, the "Portuguese Man-of-War" (Fig. 67). *Physalia* is a colonial Hydrozoan consisting of a large float (*pn.*) with a sail-like crest (*cr.*) from which a number of polyps hang down into the water. Some of these polyps are nutritive, others are tactile; some contain batteries of nematocysts, others are male reproductive zooids, and still others give rise to egg-producing medusæ.

Corals. — One group of Cœlenterates, the corals, is of especial interest because of its economic importance. The corals are found principally in the tropics. They live near the shore, which not infrequently is built up of coral skeletons. The hard parts



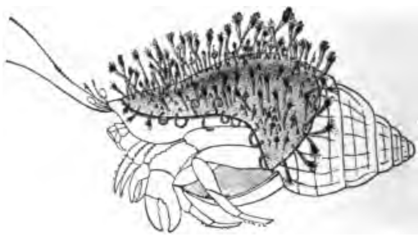


FIG. 68. Association of a hermit crab and a Cœlenterate. (From Parker and Haswell.)

FIG. 67. *Physalia*, the "Portuguese man-of-war." *cr.*, crest; *p.*, polyp; *pn.*, pneumatophore. (From Parker and Haswell after Huxley.)

of corals are composed of calcium carbonate excreted by the ectoderm cells of the polyps. So numerous are these polyps that many islands in the Pacific Ocean and many reefs near other islands consist entirely of coral rock. The precious Red Coral is found only in the Mediterranean Sea.

Symbiosis. — Symbiosis means an intimate and advantageous association between two kinds of organisms. The most common example is the lichen, which consists of two plants, an alga and a fungus. *Hydra viridis*, the green *Hydra*, derives its color from a great number of unicellular green plants, the *Zoochlorellæ*, which occupy the basal portion of the entoderm cells. These green algæ manufacture starch in the presence of light, and, during this process, liberate oxygen which is of advantage to the polyp. Probably the *Hydra* also obtains food from these algæ. The security and carbon dioxide furnished by the protecting cells of the polyp compensate the algæ for the food and oxygen they provide.

A most complicated illustration of symbiosis is that of certain *hermit crabs* with *sea anemones*. The hermit crab lives in the shell of a large salt-water snail. As soon as a suitable shell is found, the hermit crab takes possession. It then hunts about until it finds a sea anemone, which it places upon the shell just above the opening. Often the anemone completely covers the hermit crab's house. The advantage to the sea anemone in this partnership lies in the greater chances it has for proper food conditions, since it is carried about from place to place by the crab. The benefits to the latter are of a peculiar character. Figure 68 shows a Cœlenterate colony, *Hydractinia*, consisting of nutritive polyps with tentacles, reproductive individuals bearing a circle of medusoid buds, spine-like protective members, and bordering the edge of the shell, a row of threadlike defensive polyps provided with stinging cells. When the hermit crab is attacked, these stinging cells are shot into the enemy, which is thus frequently driven away. In this way the Cœlenterate benefits its associate.

CHAPTER IX

SPONGES, FLAT WORMS, AND ROUND WORMS[1]

1. SPONGES — GRANTIA

(*Grantia ciliata* Flem.)

FIG. 69. A simple sponge. (After Minchin in Lankester's Treatise.)

Grantia (Fig. 69) is a simple sponge inhabiting the salt water along the coast of the New England states just below the low-tide mark. Here it is found attached by one end to rocks and other solid objects. Unlike *Hydra*, *Grantia* is *permanently attached*, never moving from place to place as an adult. Its distribution in space is effected during the early embryonic stages, at which time cilia are present, enabling it to swim about.

Grantia varies in length from one half an inch to almost an inch, and resembles in shape a slender vase that bulges slightly near the center. The distal end of the animal opens to the exterior by a large *excurrent pore*, the *osculum*. This opening is surrounded on all sides by a circlet of long straight needles called *spicules*. Smaller spicules protrude from other parts of the body, giving the

[1] Since it was impossible to include in this book detailed discussions of types from every phylum of the animal kingdom, many groups are not represented. In this chapter three animals are briefly described in order that the step from a simple Cœlenterate, like *Hydra*, to a complex Annelid, like the earthworm, may not be too abrupt. The sponges, flat worms, and round worms possess certain organs that help the student to understand the structure and functions of similar organs in more complex animals.

animal a ciliated appearance. The body wall is perforated by numerous *incurrent pores*. This characteristic has suggested the name Porifera (Lat. *porus*, a pore, and *ferre*, to bear) to members of this phylum.

Structure. — A specimen of *Grantia* split longitudinally (Fig. 70) shows the body to be a hollow sac, one large central cavity, the *cloaca*, being present. The body wall is honeycombed by a great many canals; some of these, the *radial canals*, open to the cloacal cavity through minute pores, the *apopyles*, and end blindly near the outer surface; others, the *incurrent canals*, open to the outside through small incurrent pores or *ostia*, and end blindly near the inner surface of the body wall; still other canals, the *prosopyles*, even smaller than those already noted, connect the radial with the incurrent canal. Figure 70 shows in longitudinal section the cloacal cavity of a simple sponge, at the bottom of which are the openings of the radial canals; the body wall is seen to be crowded with both radial and incurrent canals, which have been cut lengthwise. The relations of the various canals to one another are shown in Figure 75; here the arrows indicate the direction of the current

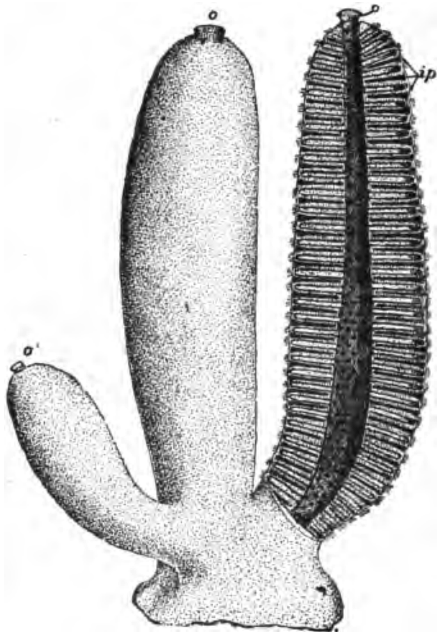


FIG. 70. Longitudinal section of a simple sponge. *ip.*, incurrent pores; *o.*, osculum. (From Parker and Haswell.)

of water, which enters the incurrent canal, passes through the prosopyles into the radial canal, and thence into the cloacal cavity, finally escaping from the body by way of the osculum.

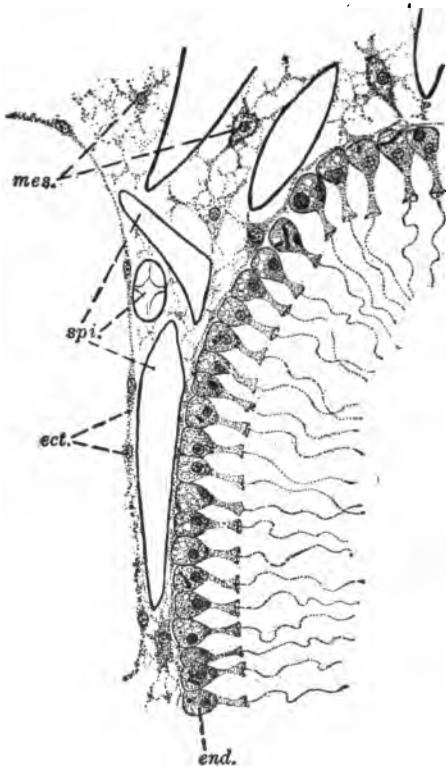


FIG. 71. Part of the body of *Grantia*. *ect.*, ectoderm; *end.*, entoderm; *mes.*, mesoderm; *spi.*, spicules. (From Dahlgren and Kepner.)

The surface area of the epithelium covering the body, and lining the internal cavities, is enormously increased by the canal system.

Grantia is an animal possessing an outer dermal layer of cells, an inner gastral epithelium, and a middle region containing cells of several varieties (Fig. 71). The *dermal epithelium* (Fig. 71, *ect.*) covers the entire outer surface of the body, and lines the incurrent canals. It is composed externally of a single layer of flat cells. Wherever prosopyles occur connecting the incurrent with the radial canals, a single large dermal cell, termed a porocyte, is present. The *porocytes* are derived from cells of the dermal epithelium. They are large and granular, and frequently exhibit ameboid movements. The prosopyle is an intracellular perforation of the porocyte. Cells, called *sclero-*

blasts, which produce spicules, are also considered constituents of the dermal layer.

The *inner epithelium* lines the cloacal cavity and the radial canals. In the latter it consists of one layer of collared flagellated cells (Fig. 71, end.), termed *choanocytes.* No collar cells are present in the epithelium lining the cloacal cavity. The flagella of the collar cells create the current of water which is continually flowing through the body wall into the cloacal cavity and out of the osculum.

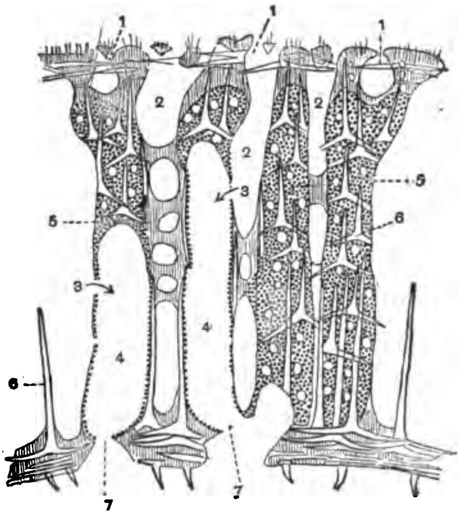


FIG. 72. Section of a portion of *Grantia.* *1*, openings of incurrent canals; *2*, incurrent canal; *3*, prosopyle; *4*, radial canal; *5*, choanocytes; *6*, spicules; *7*, opening of radial canal. (From Shipley and MacBride after Dendy.)

The *middle region* of the body wall is not so definite nor firm in structure as are the outer and inner epithelia, but, nevertheless, it is considered a distinct cellular layer. *Ameboid wandering cells,* which ingest food or act as storage cells, are found here, as well as the *reproductive cells* which always arise in the middle layer.

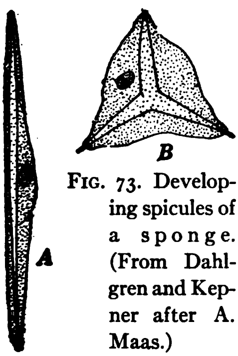


FIG. 73. Developing spicules of a sponge. (From Dahlgren and Kepner after A. Maas.)

The soft body wall of *Grantia* (Fig. 72) is supported and protected by a skeleton composed of a great number of *spicules* of

other animals can be discussed successfully. The character of the object to which sponges are attached causes them to assume exceedingly irregular shapes, the rocks being frequently incrusted

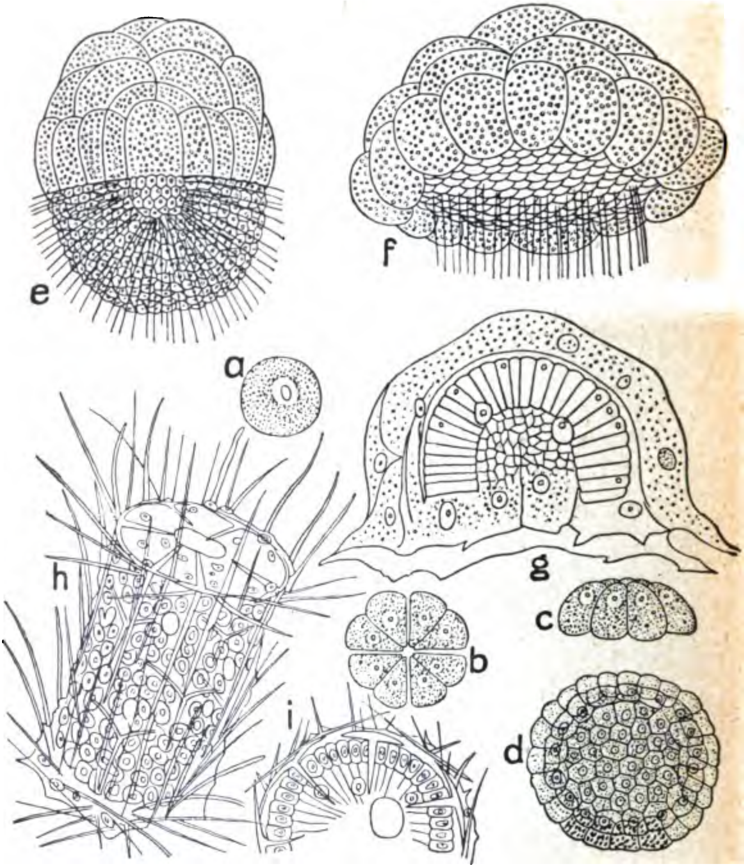
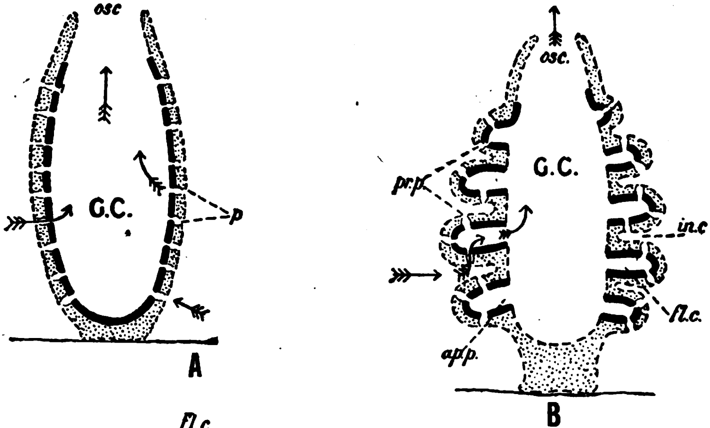


FIG. 74. Development of a simple sponge (*Sycon raphanus*). *a*, ovum; *b*, *c*, ovum segmented; *d*, blastula; *e*, amphiblastula; *f*, commencement of invagination; *g*, gastrula attached; *h*, *i*, young sponge. (From Parker and Haswell after Schulze.)

by indefinite masses of spongy tissue. This makes it difficult to decide what constitutes an individual sponge. Perhaps the best way to separate one from another is to consider all of the tissue surrounding one osculum as a single individual.



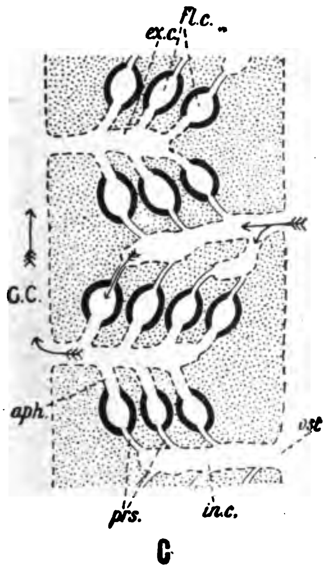


FIG. 75. Types of canal systems of sponges. The arrows indicate the direction of the current of water. The thick black line represents the gastral layer, the dotted portion, the dermal layer. *ap. p.*, apopyle; *ex. c.*, excurrent canal; *fl. c.*, flagellated chamber; *G C*, gastral cavity (cloaca); *in. c.*, incurrent canal; *osc.*, osculum; *ost.*, ostia; *pr. p.*, prosopyle. (After Minchin in Lankester's Treatise.)

Canal System. — The canal systems of sponges may be grouped under three types; the first (Fig. 75, A) consists of incurrent pores (p), a gastral cavity (GC), and an osculum ($osc.$).

The second type (Fig. 75, B) is more complicated; the water flows through the dermal pores (ostia) into the incurrent canals (*inc.*); then through the chamber pores (prosopyles, *pr. p.*) into the radial canals (*fl. c.*); from here it is propelled by the flagella of the choanocytes into the gastral cavity (*GC*), finally passing out through the osculum (*osc.*). In the third type (Fig. 75, C) there are three distinct parts, (1) the water passes through the dermal ostia (*ost.*) and by way of incurrent canals (*inc.*) reaches (2) a number of small chambers (*fl. c.*) lined with choanocytes, thence it is carried through (3) an excurrent system (*exc.*) to the gastral cavity (*GC*), and finally out of the osculum.

The *skeletons* of sponges are composed of spicules and *spongin.* The former are secreted by cells of the dermal layer, and consist of calcite and silica. The spongin is an organic substance.

Reproduction. — Reproduction is either asexual or sexual. By the *asexual* method there are produced buds and gemmules. *Buds* may be set free to take up a separate existence, or may remain attached to the parent sponge, aiding in the formation of a complex assemblage of individuals. *Gemmules* occur in the fresh-water sponge, *Spongilla,* and several marine species. A number of cells in the middle layer of the body wall gather into a ball and become surrounded by protecting spicules. These gemmules are formed in the autumn just before the death of the adult sponge. In the spring they develop into new sponges. They are of value in carrying the race through a period of adverse conditions, such as the winter season. *Sexual reproduction* takes place essentially as described for *Sycon* on page 149.

Pieces of sponges are capable of *regenerating* entire animals. This characteristic enables sponge-growers to plant a bed of sponges by scattering small pieces over the bottom of the sea in favorable places. After a period of several years, animals of commercial value may be gathered, and a new lot of "slips" set out.

Embryology. — The principal stages of sponge embryology may be presented briefly as follows: —

(1) The fertilized egg divides to form a group of cells.

(2) These cells become separated into three classes: (*a*) flagellated outer cells, (*b*) large non-flagellated cells either within or at the posterior pole, and (*c*) undifferentiated cells between the other two varieties. This embryo swims about with the aid of its flagella.

(3) The larva comes to rest, and the flagellated cells pass to the interior, while the large non-flagellated cells migrate to the outside.

(4) The flagellated cells become the choanocytes of the adult; the large non-flagellated cells become differentiated into the three strata of the dermal layer; and the cells of the middle region remain as the ameboid wandering cells and reproductive cells of the full-grown sponge.

2. Flat Worms — Planaria

(*Planaria maculata* Leidy)

External Features. — *Planaria maculata* (Fig. 76) is a flat worm found only in fresh water, usually clinging to the underside of logs or stones. Like most of the members of the Phylum Platyhelminthes, its body is extremely flattened dorso-ventrally, and is bilaterally symmetrical. *Planaria* is broad and blunt at the anterior, and pointed at the posterior end. The *length* of an adult specimen may reach half an inch. The body contains so much coloring matter as to make the location of the internal

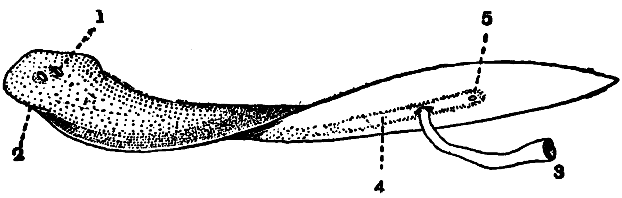


Fig. 76. *Planaria polychroa.* *1*, eye; *2*, side of head; *3*, proboscis; *4*, pharynx sheath; *5*, genital pore. (From Shipley and MacBride.)

structures difficult to determine in a living animal. In order to study *Planaria* successfully in the laboratory, the soft, contractile body is usually placed on a slide, and then pressed out slightly with a cover glass.

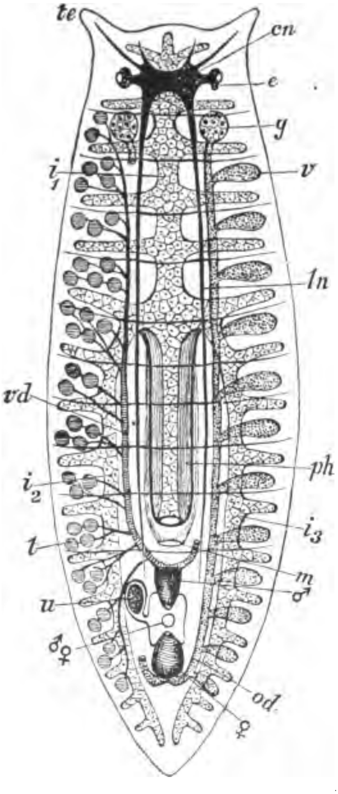


FIG. 77. Anatomy of *Planaria*. *cn*, brain; *e*, eye; *g*, ovary; i_1, i_2, i_3, branches of intestine; *ln*, lateral nerve; *m*, mouth; *ph*, pharynx; *od*, oviduct; *t*, testis; *u*, uterus; *v*, yolk glands; *vd*, vas deferens; ♂, penis; ♀, vagina; ♂, ♀, common genital pore. (From Lankester's Treatise after V. Graff.)

A pair of *eye spots* (Fig. 76, *1*) are present on the dorsal surface near the anterior end. The *mouth* is in a peculiar position near the middle of the ventral surface. From it the muscular *proboscis* (*3*) may extend. Posterior to the mouth is a smaller opening, the *genital pore* (*5*). The surface of the body is covered with *cilia*, which propel the animal through the water. This is not the only method of locomotion, since muscular contraction is also effective.

Structure. — A study of the structure of the adult and of the early embryonic stages shows *Planaria* to be a *triploblastic* animal possessing the three germ layers, ectoderm, mesoderm, and entoderm, from which several systems of organs have been derived. There are well-developed muscular, nervous, digestive, excretory, and reproductive systems; these are constructed in such a way as to function

without the coordination of a circulatory system, respiratory system, cœlom, and anus.

Digestive System. — The digestive system (Fig. 77) consists of a *mouth* (*m.*), a *pharynx* (*ph.*) lying in a muscular sheath, and an *intestine* of three main trunks (i, i_2, i_3) and a large number of small lateral extensions. The muscular pharynx can be extended as a proboscis (Fig. 76, *3*); this facilitates the capture of food. Digestion is both *intercellular* and *intracellular*, *i.e.* part of the food is digested in the intestinal trunks by secretions from cells in their walls; whereas other food particles are engulfed by pseudopodia thrust out by cells lining the intestine, and are digested inside of the cells in vacuoles. The digested food is absorbed by the walls of the intestinal trunks, and, since branches from these penetrate all parts of the body, no circulatory system is necessary to carry nutriment from one place to another. As in *Hydra*, no *anus* is present, the *fæces* being ejected through the mouth.

Excretory System. — The excretory system comprises a pair of longitudinal, much-coiled tubes, one on each side of the body; these are connected near the anterior end by a transverse tube, and open to the exterior by two small pores on the dorsal surface. The longitudinal and transverse trunks give off numerous finer tubes which ramify through all parts of the body, usually ending in a *flame cell*. The flame cell (Fig. 78) is large and hollow, with a bunch of flickering cilia (*c*) extending into the central cavity (*e*). Since it communicates only with the excretory tubules it is considered excretory in function, though it may also carry on respiratory activities.

Muscular System. — The power of changing the shape of its body, which may be observed when *Planaria* moves from place to place, lies principally in three sets of muscles, a circular layer just beneath the ectoderm, external and internal layers of longitudinal muscle fibers, and a set of oblique fibers lying in the mesoderm.

Nervous System. — *Planaria* possesses a well-developed nerv-

ous system, consisting of a bilobed mass of tissue just beneath the eye spots, called the ***brain*** (Fig. 77, *cn*) and two lateral ***longitudinal nerve cords*** (*ln*) connected by transverse nerves. From the brain, nerves pass to various parts of the anterior end of the body, imparting to this region a highly sensitive nature.

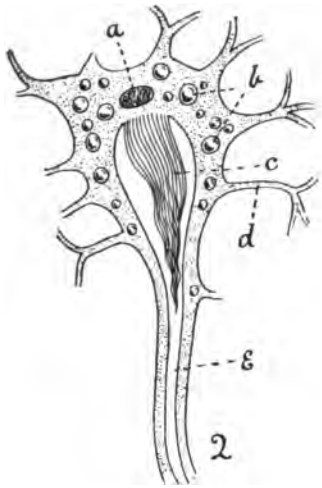


FIG. 78. Flame cell of *Planaria*. *c*, cilia; *e*, opening into excretory tubule. (From Lankester's Treatise.)

REPRODUCTIVE SYSTEM.—Reproduction is by *fission* or by the sexual method. Each individual possesses both male and female organs, *i.e.* is *hermaphroditic*. The *male organs* may be located easily in Figure 77; they consist of numerous spherical *testes* (*t.*) connected by small tubes called *vasa deferentia* (*vd.*); the *vas deferens* from each side of the body joins the *cirrus* or *penis* (♂), a muscular organ which enters the *genital cloaca*. A *seminal vesicle* lies at the base of the penis, also a number of unicellular *prostate glands*. Spermatozoa originate in the testes, and pass, by way of the *vasa deferentia*, into the seminal vesicle, where they remain until needed for fertilization. The *female reproductive organs* comprise two *ovaries* (*g*), two long *oviducts* (*od.*) with many yolk glands (*v*) entering them, a *vagina* (♀), which opens into the genital cloaca, and the *uterus*, which is also connected with this cavity. The *eggs* originate in the ovary, pass down the oviduct, collecting yolk from the yolk glands on the way, and finally reach the uterus. Here fertilization occurs, and *cocoons* are formed, each containing from four to more than twenty eggs, surrounded by several hundred yolk cells. The *development* of the egg is illustrated and explained in Figure 79.

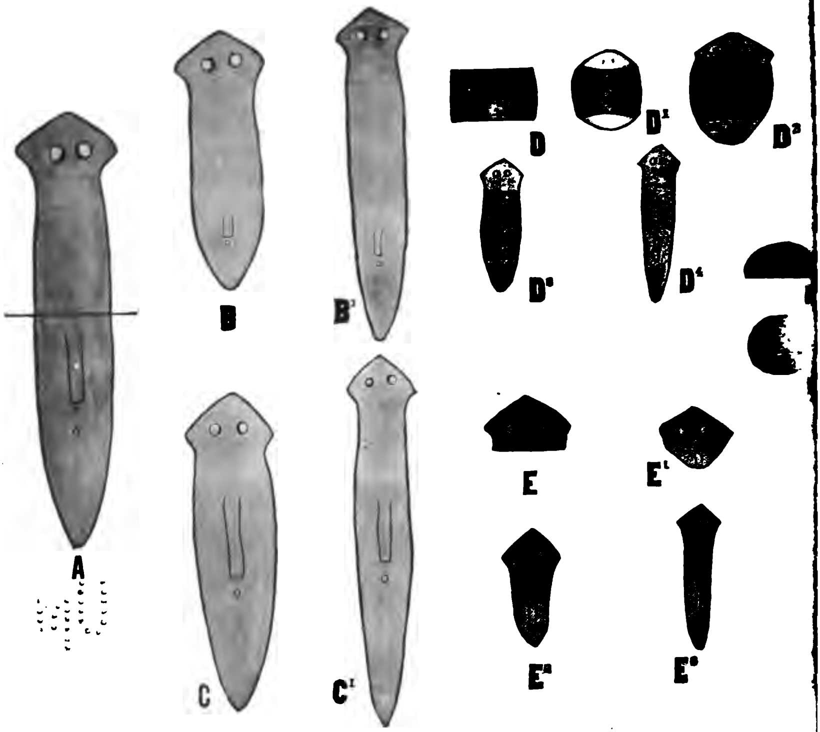


FIG. 80. Regeneration of *Planaria maculata*. A, normal worm; B, B^1, regeneration of anterior half; C, C^1, regeneration of posterior half; D, crosspiece of worm; D^1, D^2, D^3, D^4, regeneration of same; E, old head; E^1, E^2, E^3, regeneration of same; F, F^1, regeneration of new head on posterior end of old head. (From Morgan.)

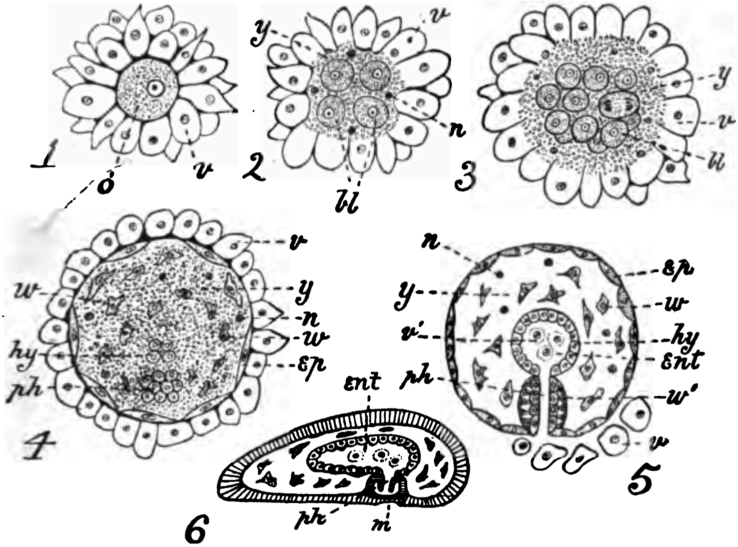


Fig. 79. Development of *Planaria lactea.* *1*, egg (*o*) surrounded by yolk (*v*); *2*, four blastomeres from segmented egg; *3*, later stage; more blastomeres (*bl*); *4*, much later stage, differentiation of blastomeres into ectoderm (*ep*), entoderm (*hy*), a provisional pharynx (*ph*), and wandering cells (*w*); *5*, cellular differentiation more advanced; *ep*, ectoderm; *ent*, primitive gut; *hy*, entoderm; *ph*, pharynx; *6*, embryo changes shape to a flattened ovoid, *ent*, primitive gut; *m*, mouth; *ph*, pharynx. (From Lankester after Hallez.)

Regeneration. — Planarians show remarkable powers of regeneration. If an individual is cut in two (Fig. 80, A), the anterior end will regenerate a new tail (B, B′), while the posterior part develops a new head (C, C′). A crosspiece (D) will regenerate both a head at the anterior end, and a new tail at the posterior end (D'–D^4). The head alone of a Planarian will grow into an entire animal (E—E^3). Pieces cut from various parts of the body will also regenerate completely. No difficulty is experienced in grafting pieces from one animal upon another, and many curious monsters have been produced in this way.

Flat Worms in General

Flat worms are usually separated into three classes.

Class 1. — Turbellaria. Flat worms with ciliated epidermis and digestive cavity; mostly non-parasitic. Example, *Planaria*.

Class 2. — Trematoda. Flat worms without ciliated epidermis; digestive apparatus well developed; ecto- or endoparasitic. Example, liver fluke of sheep.

Class 3. — Cestoda. Flat worms without ciliated epidermis and digestive apparatus; endoparasitic. Example, tapeworm.

Planaria shows the principal features characteristic of flat worms; but there must necessarily be wide diversity in structure among the members of a phylum composed of both free-living and parasitic forms. The free-living flat worms, such as *Planaria*, probably are more nearly like the ancestors of this phylum than the parasitic species, since the latter have undoubtedly become degenerate with respect to certain structures, and more specialized with respect to others, because of their modified habits of life. From a study of *Planaria*, therefore, we can gain some idea of what kind of an animal gave rise to the flat worms.

In the first place definite *bilateral symmetry* is exhibited here. Flat worms thus show an advance in this respect over the more simple radial symmetry of Cœlenterates. A second point to be noted is the presence of a distinct mesoderm between the ectoderm and entoderm. This mesoderm consists of muscle cells and connective tissue. As in the Cœlenterates, however, there is but one body cavity, represented by the digestive system, though the genital sacs may represent a second cavity, known as the *cœlom*, which is well developed in more complex animals.

The *digestive apparatus* is not a simple blind sac, as in *Hydra*, but consists of several large branches, each with many smaller side pouches entering it, the whole being modified to transport nutriment to all parts of the body, a circulatory system being lacking. An anus, however, is absent, the ingestion of food and

the egestion of fæces taking place through a single aperture, the mouth.

The *nervous system* of flat worms shows a marked advance, especially in concentration, over that of the Cœlenterates. The presence of a brain near the end of the body directed forward in moving is what would be expected, since this end receives all sensations first, and nerve cells would be developed in the region of greatest stimulation.

TABLE V

THE CHARACTERS OF HYDRA AND PLANARIA CONTRASTED

Character	Hydra	Planaria
Symmetry	Radial	Bilateral
Germ layers	Diploblastic	Triploblastic
Digestive system	Cœlenteric cavity	Pharynx and branched intestine
Cœlom	Absent	May be represented by genital sacs
Excretory system	None	Complicated system of tubes, ending in flame cells and opening to exterior
Nervous system	Network of nerve cells	Nerve cells concentrated into brain and nerve cords
Muscular system	Processes of ectoderm and entoderm cells	Muscle fibers with no other function, from mesoderm cells
Reproductive system	No accessory reproductive organs	A complicated reproductive apparatus

Excretory organs and a complicated *reproductive system* make their appearance in this phylum. The *muscle fibers* of *Hydra* are simple specializations of cells that perform other functions; but in *Planaria*, cells are set aside for no other purpose than to give a high degree of contractility to the body. These cells form distinct bands of circular, longitudinal, and oblique muscles. Table V contrasts the structures of *Hydra* and *Planaria*. In this way a clear idea of the advance in complexity exhibited by the latter may be gained.

3. Round Worms — Ascaris

(*Ascaris lumbricoides* Linn.)

External Features. — *Ascaris* is a round worm parasitic in the intestines of pigs, horses, and man. The sexes are separate. The female, being the larger, measures from five to eleven inches in *length* and about one fourth of an inch in *diameter*. The body is light brown in *color;* it has a dorsal and a ventral white narrow stripe running its entire length and a broader *lateral line* is present on either side. The anterior end possesses a *mouth opening*, surrounded by one dorsal and two ventral *lips*. Near the posterior end is the *anal opening*, from which, in the male, extends *penial setæ* of use during copulation. The male can be distinguished from the female by the presence of a bend in the posterior part of the body.

Internal Anatomy. — If an animal is cut open along the dorsal line (Fig. 81), it will be found to contain a straight alimentary canal, and certain other organs, lying in a central cavity, the *cœlom*, a cavity met with now for the first time. The *alimentary canal* (*2*) is very simple, since the food is taken from material already digested by the host whose intestine the worm inhabits. It opens at the posterior end through the *anus*, which is not present in members of the phyla already discussed. A muscular *pharynx* (*1*) draws the fluids into the long non-muscular *intestine* (*2*),

through the walls of which the nutriment is absorbed. Just before the anal opening is reached, the intestine gradually becomes smaller; this portion is known as the *rectum*.

The *excretory system* consists of two longitudinal canals (Fig. 81, *7*), one in each lateral line; these open to the outside by a single pore (*8*) situated near the anterior end in the ventral body wall.

A ring of *nervous tissue* surrounds the pharynx and gives off two large nerve cords, one dorsal, the other ventral, and a number of other smaller strands and connections.

The *male reproductive organs* are a single coiled thread-like *testis*, from which a *vas deferens* leads to a wider tube, the *seminal vesicle;* this is followed by the short muscular *ejaculatory duct* which opens into the rectum. In the *female* lies a Y-shaped reproductive system. Each branch of the Y consists of a coiled thread-like *ovary* (Fig. 81, *3*) which is continuous with a larger canal, the *uterus* (*4*). The uteri of the two branches unite into a short muscular tube, the *vagina* (*5*), which opens to the outside through the *genital aperture* (*6*). *Fertilization* takes place in the uterus. The egg is then surrounded by a shell of chitin, and

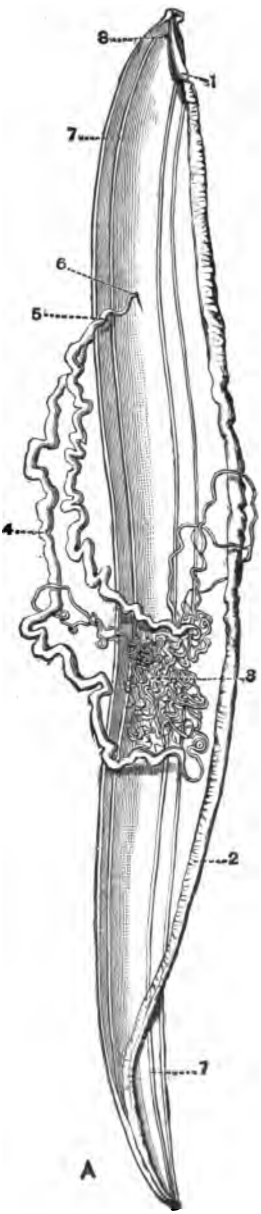


FIG. 81. Female *Ascaris lumbricoides*, cut open to show internal organs. *1*, pharynx; *2*, intestine; *3*, ovary; *4*, uterus; *5*, vagina; *6*, genital pore; *7*, excretory tube; *8*, excretory pore. (From Shipley and MacBride.)

passes out through the genital pore. The chitinous eggshell prevents the digestion of the egg within the intestine of the host.

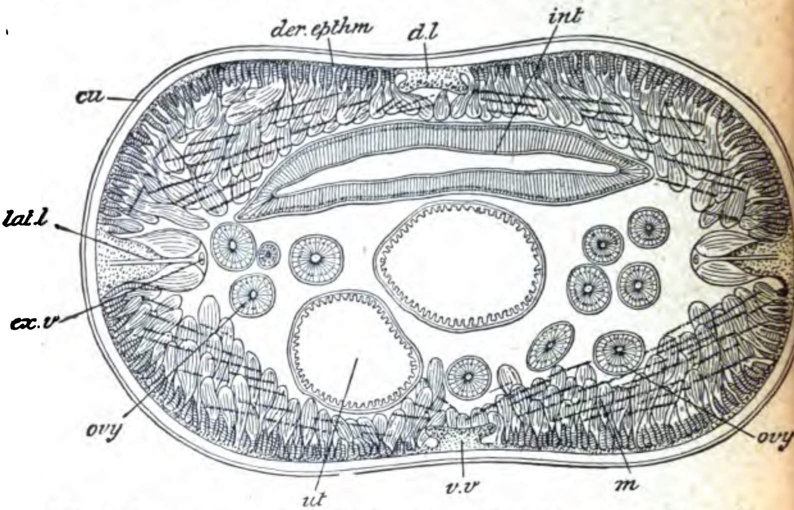


FIG. 82. Transverse section of *Ascaris lumbricoides*. *cu.*, cuticle; *dl.*, dorsal line; *der. epthm.*, epidermis; *ex. v.*, excretory tube; *int.*, intestine; *lat. l.*, lateral line; *m.*, muscular layer; *ovy.*, ovary; *ut.*, uterus; *v. v.*, ventral line. (From Parker and Haswell after Vogt and Yung.)

The relations of the various organs to one another, as well as the structure of the body wall, and the character of the cœlom, are shown in Figure 82, which is a transverse section of a female specimen of *Ascaris lumbricoides*. The body of the worm should be considered as consisting of two tubes, one, the intestine (*int.*), lying within the other, the body wall; while between them is a cavity, the *cœlom*, in which lie the reproductive organs (*ovy.* and *ut.*).

The *body wall* is composed of several layers, an outer chitinous cuticle (*cu.*), a thin layer of ectoderm (*der. epthm.*) just beneath it, and a thick stratum of longitudinal muscle fibers (*m.*), mesodermal in origin, lining the cœlom. Thickenings of the ectoderm form the dorsal (*d. l*), ventral (*v. v*) and lateral (*lat. l*) lines. In each

of the last-named lies one of the longitudinal excretory tubes (*ex. v.*). The nerve cords are also embedded in the body wall.

The *intestine* consists of a single layer of columnar cells, the entoderm, coated both within and without by a thin cuticle.

The *cœlom* of *Ascaris* differs from that of the higher animals in several respects. Typically the cœlom is a cavity in the mesoderm lined by an epithelium; into it the excretory organs open, and from its walls the reproductive cells originate. In *Ascaris* the so-called cœlom is lined only by the mesoderm of the body wall, there being no mesoderm surrounding the intestine. Furthermore, the excretory organs open to the exterior through the excretory pore, and the reproductive cells are not derived from the cœlomic epithelium. The body cavity of *Ascaris*, therefore, differs structurally and functionally from that of a true cœlom, but nevertheless is similar in many respects.

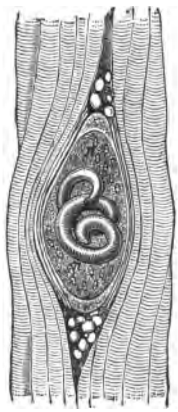


FIG. 83. *Trichina spiralis* encysted among muscle fibers. (From Shipley and MacBride after Leuckart.)

ROUND WORMS IN GENERAL

The round worms belong to the Phylum Nemathelminthes. They are mostly parasitic; only a comparatively small number are free-living, inhabiting damp earth or fresh and salt water. Among the most interesting round worms is the parasite, *Trichina spiralis* (Fig. 83), which is often found encysted in the muscles of the pig. When insufficiently cooked pork infested by *Trichina* is eaten by man, the young parasites become mature in the intestine, and burrow through its walls, causing a disease known as Trichinosis.

CHAPTER X

THE EARTHWORM AND ANNELIDS IN GENERAL

1. The Earthworm

(*Lumbricus terrestris* Linnæus)

The earthworm, *Lumbricus terrestris*,[1] lives in the ground where the soil is not too dry or sandy, coming to the surface only at night or after a rain. The burrows are cylindrical and penetrate to a depth of from six inches to several feet. Evidences of the presence of earthworms are found in the little heaps of black earth, called "castings," which strew the ground, being especially noticeable early in the morning. These castings are really the fæces cast out from the alimentary canal of the worm. Darwin (139) estimated that more than eighteen tons of earthy castings are carried to the surface in a single year on one acre of ground, and in twenty years a layer three inches thick would be transferred from the subsoil to the surface. This continuous honeycombing of the soil makes the land more porous, and insures the better penetration of moisture, and the continuous working over of the surface layers of earth also helps to make the soil more fertile.

External Features. — *Lumbricus terrestris* reaches a *length* of from six inches to as much as a foot. It is capable of pronounced extensions and contractions, so that the length of an individual varies, as does also its diameter. Although its body is cylindroid it is possible to recognize dorsal, ventral, and lateral surfaces. Movement takes place in a definite direction, the advancing

[1] This is one of many species of earthworms. In many parts of this country the species *Allolobophora* (*Helodrilus*) *longa* or one of the species of Diplocardia are more abundant in cultivated soil.

portion being known as the anterior, the hinder portion as the posterior end. The principal axis of the body is antero-posterior, and, since the chief organs both external and internal lie half on one side and half on the other side of a median plane, the worm is said to be bilaterally symmetrical.

A noticeable feature of the earthworm is its division into a large number of similar rings by grooves extending around the body at short intervals. These rings are termed *segments*, *somites*, or *metameres*, and the body is said to be segmented or to have a metameric structure. The earthworm and many of its near relatives differ in this respect from the unsegmented flat worms and round worms, such as *Planaria* and *Ascaris*. The somites are not exactly alike. The anterior lobe extending above and beyond the mouth, and backward on the dorsal surface intersecting the first segment is not a true somite; it is known as the *prostomium*. It has been found that not only external structures, but also internal organs, bear a constant relation to the segments; for this reason the somites have been numbered, beginning with the one just back of the prostomium. In mature worms the six or seven somites, XXXI or XXXII to XXXVII, are swollen on their dorsal and lateral surfaces, producing a saddle-shaped enlargement known as the *clitellum*, of use during reproduction.

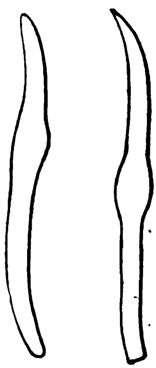


FIG. 84. Two setæ of *Lumbricus*, highly magnified. (From Parker and Haswell.)

If an apparently smooth earthworm is drawn through the fingers from its anterior end toward the tail, it feels rough to the touch. This is caused by small *f*-shaped chitinous bristles, called *setæ* (Fig. 84), four pairs of which extend outward from epidermal sacs in every somite except the first and last. Each pair may be moved by retractor and protractor muscles. The arrangement of the setæ is shown in the right-hand half of the section in Figure

85, *set.* New setæ may be produced by any one of a number of cells lying at the bottom of the epidermal sacs. On mature worms the setæ on somite XXVI are enlarged and modified as sexual setæ.

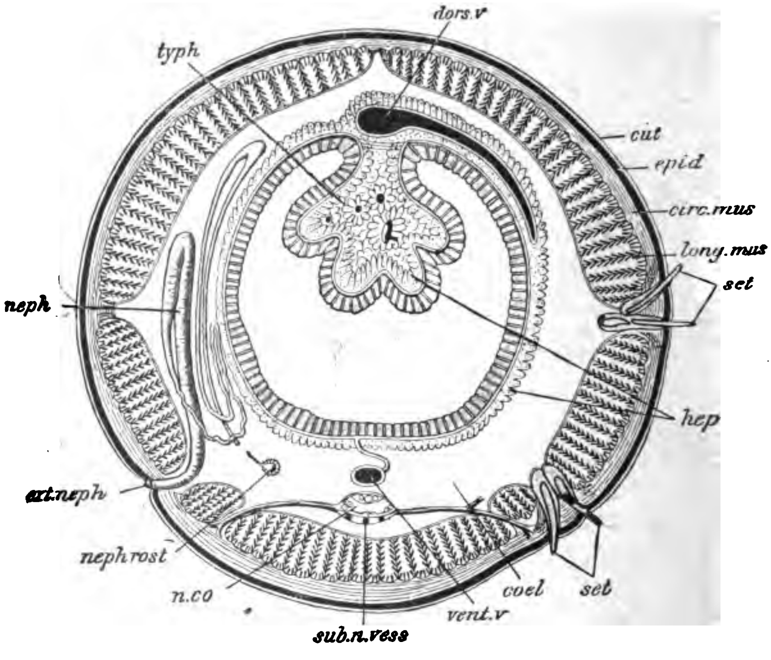


FIG. 85. Transverse section through the middle region of the body of *Lumbricus*. *circ. mus.*, circular muscle fibers; *cœl.*, cœlom; *dors. v.*, dorsal vessel; *epid.*, epidermis; *ext. neph.*, nephridiopore; *hep.*, chloragogen cells; *long. mus.*, longitudinal muscles; *neph.*, nephridium; *nephrost.*, nephrostome; *n. co.*, nerve cord; *set.*, setæ; *sub. n. vess.*, sub-neural vessel; *typh.*, typhlosole; *vent. v.*, ventral vessel. (From Parker and Haswell after Marshall and Hurst.)

The outer covering of the body is a thin transparent membrane, the *cuticle* (Fig. 85, *cut.*), which is secreted by the cells lying just beneath it. The cuticle protects the body wall from physical

or chemical injury; numerous fine *pores* allow the secretions from unicellular glands to pass through (Fig. 86). Under the microscope it is seen to be marked with very fine *striæ* which cross one another; they cause the surface of the body to appear iridescent.

A number of *external openings* of various sizes allow the entrance of food into the body, and the exit of fæces, excretory products, reproductive cells, etc. (1) The *mouth* is a crescentic

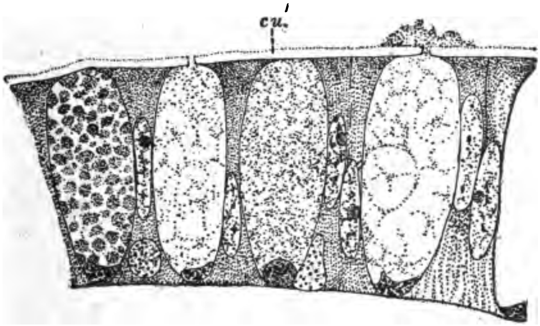


FIG. 86. Vertical section of a bit of epidermis of the earthworm. Four mucus cells in different stages of secretion. Mucus is passing through one of the two pores in the cuticle, *cu.* (From Dahlgren and Kepner.)

opening situated in the ventral half of the first somite; it is overhung by the prostomium. (2) The oval *anal aperture* lies in the last somite. (3) The openings of the sperm ducts or *vasa deferentia* are situated one on either side of somite XV. They have swollen lips; a slight ridge extends posteriorly from them to the clitellum. (4) The openings of the *oviducts* are small round pores one on either side of somite XIV; eggs pass out of the body through them. (5) The openings of the *seminal receptacles* appear as two pairs of minute pores concealed within the grooves which separate somites IX and X, and X and XI. (6) A pair of *nephridiopores* (Fig. 85, *ext. neph.*), the external apertures of the excretory organs, open on every somite except the first three and the last. They are usually situated immediately anterior to the outer seta of the inner pair. (7) The *body cavity* (Fig. 85,

coel.) communicates with the exterior by means of *dorsal pores*. One of these is located in the mid-dorsal line at the anterior edge of each somite frcm VIII or IX to the posterior end of the body.

General Internal Anatomy. — If a specimen is cut open from the anterior to the posterior end by an incision passing through the body wall a trifle to one side of the mid-dorsal line, a general view of the internal structures may be obtained (Fig. 87). As in *Ascaris*, the body is essentially a *double tube* (Fig. 85), the *body wall* constituting the outer, the straight *alimentary canal*, the inner; between the two is a cavity, the *cœlom*. The external segmentation corresponds to an internal division of the cœlomic cavity into compartments by means of partitions, called *septa*, which lie beneath the grooves. These septa are absent in *Ascaris*. The alimentary canal passes through the center of the body, and is suspended in the cœlom by the partitions. Septa are absent between somites I and II, and incomplete between somites III and IV, and XVII and XVIII. The walls of the cœlom are lined with an epithelium, termed the *peritoneum*. The cœlomic cavity is filled with a colorless fluid which flows from one compartment to another when the body of the worm contracts. In somites IX to XVI are the *reproductive organs* (Fig. 93); running along the upper surface of the alimentary canal is the *dorsal blood vessel* (Fig. 85, *dors. v.*); and just beneath it lie the *ventral blood vessels* (*vent. v.*) and *nerve cord* (*n. co.*).

Body Wall. — The strata of the body wall are as follows (Fig. 85): (1) an outer noncellular covering, the *cuticle* (*cut.*); (2) an *epidermis* (*epid.*) composed of two cellular layers, an outer stratum consisting of gland, interstitial, and sense cells, and an inner stratum of very small cells; (3) a layer of *circular muscle fibers* (*circ. mus.*) running around the body, each fiber being long, pointed at both ends, and longitudinally striated; (4) a thick layer of muscle fibers running lengthwise of the body and appearing in cross section to be arranged in featherlike groups (*long. mus.*); (5) the innermost layer, the cœlomic epithelium or perito-

neum, a thin stratum of flattened cells lining the cœlom. The *gland cells* of the epidermis (Fig. 86) are called "goblet cells" because of their shape; they secrete the mucus which helps to keep the surface of the worm moist.

Digestive System. — The *alimentary canal* (Fig. 87) consists of (1) a mouth cavity or *buccal pouch* in somites I to III, (2) a thick muscular *pharynx* (*ph.*) lying in somites IV and V, (3) a narrow straight tube, the *œsophagus* (*œs.*) which extends through somites VI to XIV, (4) a thin-walled enlargement, the *crop* or *proventriculus* (*cr.*), in somites XV and XVI, (5) a thick muscular-walled *gizzard* (*giz.*) in somites XVII and XVIII, and (6) a thin-walled *intestine* (*int.*) extending from somite XIX to the anal aperture. The intestine is not a simple cylindrical tube; but its dorsal wall is infolded, forming a longitudinal ridge, the *typhlosole* (Fig. 85, *typh.*). This increases the digestive surface.

The *wall of the intestine* is composed of five layers: (1) an inner lining of ciliated epithelium, (2) a vascular layer containing many small blood vessels, (3) a thin layer of circular muscle fibers, (4) a layer consisting of a very few longitudinal muscle fibers, and (5) an outer thick coat of *chlorogogen cells* (Fig. 85, *hep.*) modified from the cœlomic epithelium. The last-named cells also cover the dorsal trunk of the vascular system and extend down into the typhlosole. The function of the chlorogogen cells is not certainly known, but it has been suggested that, since they are present about the alimentary canal, in the typhlosole, and in close proximity to the dorsal blood vessel which carries the food after absorption, they probably aid in the elaboration of food. That they have an excretory function also seems probable, since chlorogogen granules are present in the cœlomic fluid of adult worms, make their way through the body wall, especially through the dorsal pores, and pass outside of the body in the mucus (154). They also disintegrate in the cœlomic fluid, and the waste products are eliminated through the excretory organs.

At the sides of the œsophagus are three pairs of *calciferous glands* (Fig. 87, *œs. gl.*), one pair in each of the somites from X to

XII. The first pair are pouches pushed out from the alimentary canal and opening directly into the œsophagus. The other two pairs are swellings of the œsophageal wall; they have a number of small cavities which open directly through the epithelium into the œsophagus in somite XIV. Carbonate of lime is produced by these glands, and poured into the alimentary canal, where it probably neutralizes acid foods (143).

Nutrition. — FOOD. — The food of the earthworm consists principally of pieces of leaves and other vegetation, particles of animal matter, and soil. This material is gathered at night. At this time the worms are active; they crawl out into the air, and, with their tails holding fast to the tops of their burrows, explore the neighborhood.

INGESTION. — Food particles are drawn into the buccal cavity by suction produced when the pharyngeal cavity is enlarged. This is accomplished by the contraction of the muscles which extend from the pharynx to the body wall.

DIGESTION. — In the pharynx, the food receives a secretion from the pharyngeal glands; it then passes through the œsophagus to the crop, where it is stored temporarily. In the meantime the secretion from the calciferous glands in the œsophageal walls is added, neutralizing the acids. The gizzard is a grinding organ; in it the food is broken up into minute fragments by being squeezed and rolled about. Solid particles, such as rough pebbles, which are frequently swallowed, probably aid in this grinding process. The food then passes on to the intestine, where most of the digestion and absorption takes place.

Digestion in the earthworm is very similar to that of higher animals. The digestive fluids act upon *proteids*, *carbohydrates*, and *fats;* in them are special chemical compounds, called *ferments* or *enzymes*, which break up complex molecules without themselves becoming changed chemically. The three most important enzymes are (1) *trypsin*, which dissolves proteid, (2) *diastase*, which breaks up molecules of carbohydrates, and (3) *steapsin*, which acts upon fats. These three enzymes are

probably present in the digestive fluids of the earthworm. The proteids are changed into peptones, the carbohydrates into a sugar compound, and the fats are divided into glycerin and fatty acids.

ABSORPTION. — The food is now ready for absorption. This is accomplished through the wall of the intestine by a process known as *osmosis*, assisted by an ameboid activity of some of the epithelial cells. Osmosis is the passage of a liquid through a membrane.

CIRCULATION. — Upon reaching the blood, the absorbed food is carried to various parts of the body by circulation, the details of which are described in another place (pp. 174–175). Absorbed food also makes its way into the cœlomic cavity and is carried directly to those tissues bathed by the *cœlomic fluid.* In one-celled animals, and in such Metazoons as *Hydra, Planaria,* and *Ascaris* no circulatory system is necessary, since the food either is digested within the cells or comes into direct contact with them; but in large, complex animals a special system of organs must be provided to enable the proper distribution of nutriment.

ASSIMILATION, as in the types already described, is the addition of new particles among the preexisting particles of protoplasm.

Vascular System. — The blood of the earthworm is contained in a complicated system of tubes which ramify to all parts of the body. A number of these tubes are large and centrally located; these give off branches which likewise branch, finally ending in exceedingly thin tubules, the *capillaries.* The functions of this system of tubes are to carry nourishment from the alimentary canal to all parts of the body, to transport waste products, and to convey the blood to a point near the surface of the body where oxygen may be obtained and supplied to the tissues.

BLOOD. — The blood of the earthworm consists of a *plasma* in which are suspended a great number of colorless cells, called *corpuscles.* Its red color is due to a pigment termed *hæmoglobin,* which is dissolved in the plasma. In vertebrates the hæmoglobin is located in the blood corpuscles.

Blood Vessels. — Following a custom, which is so firmly established as to make its abandonment inadvisable, we shall call the blood tubes by the inappropriate name "vessels." Longi-

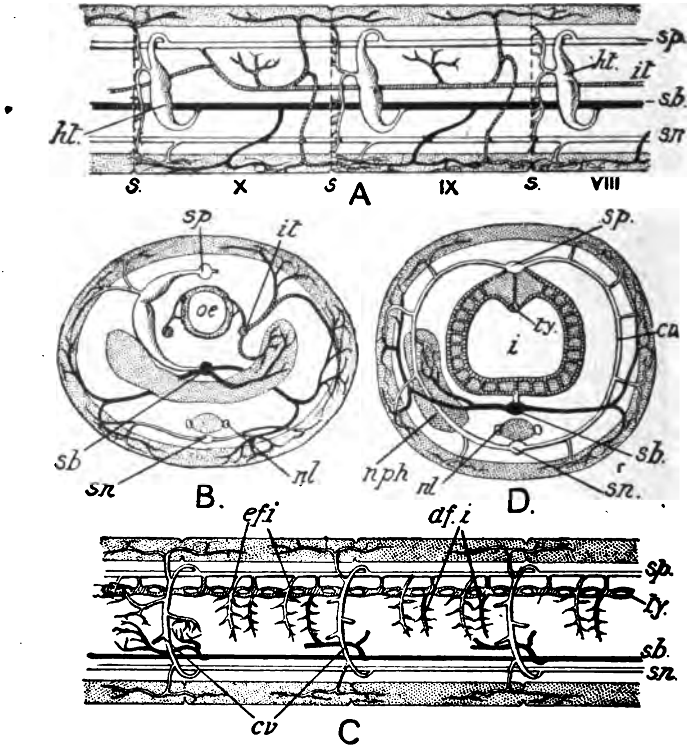


Fig. 88. Diagrams showing the arrangement of the blood vessels in the earthworm. A, longitudinal view of the vessels in somites VIII, IX, and X; B, transverse section of same region; C, longitudinal view of the vessels in the intestinal region; D, transverse section through the intestinal region; *af. i.*, afferent intestinal vessel; *c.v.*, parietal vessel; *ef. i.*, efferent intestinal vessel; *ht.*, heart; *i*, intestine; *it.*, intestino-tegumentary; *nl.*, lateral-neural vessel; *œs.*, œsophagus; *s.*, septa; *sb.*, ventral vessel; *sn.*, sub-neural vessel; *sp.*, dorsal vessel; *ty.*, typhlosolar vessel. (From Bourne after Benham.)

tudinal vessels, five in number, extend from the anterior to the posterior end of the body; these are connected with one another and with various organs by branches more or less regularly arranged.

(1) The largest and most important of the longitudinal trunks is the *dorsal* or *supra-intestinal* (Fig. 88, *sp.*), which runs along the dorsal surface of the alimentary canal, from the posterior end of the body to the pharynx.

(2) Just beneath the alimentary canal lies the *ventral* or *sub-intestinal* trunk (*sb.*). This likewise extends from the posterior end of the body to the pharynx, where it divides into many small branches.

(3) The *sub-neural* trunk (*sn.*) traverses the entire length of the body on the under side of the ventral nerve cord.

(4 and 5) The *lateral-neural* trunks (*nl.*) lie one on either side of the ventral nerve cord; they are smaller than the other longitudinal trunks.

The branches from the longitudinal trunks in the anterior part of the body differ from those in the region of the intestine. A pair of short thick tubes connect the dorsal with the ventral vessels in each of the five segments from VII to XI. These are known as *hearts* (*ht.*) because of their power of contractility. Small branches from the hearts supply the septa immediately posterior to them (Fig. 88, A). In somite X, two *intestino-tegumentary* vessels (Fig. 88, *it.* in A and B) arise, one on either side of the dorsal trunk. Each extends anteriorly, sending a pair of branches to the œsophagus in every segment from X to VI, and receiving branches from the integument and nephridia in the same somites. The ventral trunk gives rise in each segment to two vessels, one going to the nephridium, the other to the body wall (Fig. 88, D). The sub-neural receives vessels from the integument.

In the region of the intestine the dorsal is connected with the sub-neural trunk in each segment by a pair of *parietal* vessels (Fig. 88, *cv.* in C and D). The latter receive branches from the

nephridia and body wall (D). The dorsal trunk also communicates with the intestine by means of branches. Two pairs of vessels pass from it to the walls of the intestine in every segment (*ef. i.* in C). The blood is collected from the intestine by two pairs of vessels which enter a longitudinal *typhlosolar* tube (*ty.* in C). The latter is connected with the dorsal trunk by three or four short tubes in each somite. The ventral trunk in the intestinal region gives off in every segment a pair of vessels each of which divides, sending a branch to the nephridium and one to the body wall (*sb.* in D).

Structure of Blood Vessels. — The dorsal trunk and hearts determine the direction of the blood flow, since they furnish the power by means of their muscular walls. The wall of the dorsal trunk is composed of four layers: (1) an inner epithelium of thin cells, (2) a connective tissue layer; (3) a well-developed stratum of circular muscle fibers, and (4) an outer covering of chlorogogen cells. The walls of the hearts are similar in structure. Pairs of forwardly directed *valves* are situated in the dorsal trunk just behind the openings of the parietal vessels. The valves do not prevent the flow of the blood in an anterior direction, but the dorsal trunk, when constricted, is completely closed by them, making the backward flow impossible. Pairs of valves are also present in the dorsal trunk just in front of the openings of the hearts. Other valves occur in the vessels directly connected with the dorsal trunk.

The ventral trunk does not possess a layer of circular muscle fibers, and, therefore, has not the power to contract. It is strengthened by a thick layer of fibrous connective tissue. The sub-neural and lateral-neural trunks, as well as all the smaller branches, have simply an inner epithelium and an outer connective tissue layer (146).

Circulation. — The flow of blood in the blood vessels is not segmental, but *systemic*. Blood is forced forward by wave-like contractions of the dorsal trunk, beginning at the posterior end and traveling quickly anteriorly. These contractions are said

to be *peristaltic*, and have been likened to the action of the fingers in the operation of milking. The valves in the walls of the dorsal trunk prevent the return of blood from the anterior end. In somites VII to XI the blood passes from the dorsal trunk into the hearts, and is forced by them both forward and backward in the ventral trunk. The valves in the heart also prevent the backward flow. From the ventral trunk the blood passes to the body wall and nephridia. Blood is returned from the body wall to the lateral-neural trunks. The flow in the sub-neural trunk is toward the posterior end, then upward through the parietal vessels into the dorsal trunk. The anterior region receives blood from the dorsal and ventral trunks. The blood which is carried to the body wall and integument receives oxygen through the cuticle, and is then returned to the dorsal trunk by way of the sub-neural trunk and the intestinal connectives. Because of its proximity to the sub-neural trunk, the nervous system receives a continuous supply of the freshest blood (143, 146).

Respiration. — The earthworm possesses no respiratory system, but obtains oxygen and gets rid of carbon dioxide through the moist outer membrane. Many capillaries lie just beneath the cuticle, making the exchange of gases easy. The oxygen is combined with the hœmoglobin.

Excretory Organs. — Most of the excretory matter is carried outside of the body by a number of coiled tubes, termed *nephridia* (Fig. 85, *neph.*), a pair of which are present in every somite except the first three and the last. A nephridium occupies part of two successive somites; in one is a ciliated funnel, the *nephrostome* (Fig. 85, *nephrost.*), which is connected by a thin *ciliated tube* with the major portion of the structure in the somite posterior to it. Three loops make up the coiled portion of the nephridium. The thin tube mentioned above is a single row of hollow cylindrical cells placed end to end; it extends through one loop and a half, and connects with a larger tube brown in color and ciliated throughout its central cavity. This portion, known as the *middle tube*, opens into a *third tube*, which is wider, but without cilia.

Leading from the third tube to the external aperture is a large *muscular duct.* The structure of the nephrostome and of the thin tube just behind it is of particular interest. The nephrostome (Fig. 89) consists of a large crescentic central cell (*c.c.*) surrounded by a layer of ciliated marginal cells (*cp.*); these join a number of grooved cells (*cf.*) which lead to the thin ciliated tube. The central cavity of this ciliated tube is not surrounded by cells, that is, intercellular, but is intracellular, passing directly through the cells. The tube thus resembles a drainpipe, the sections of which are represented by single cells placed end to end.

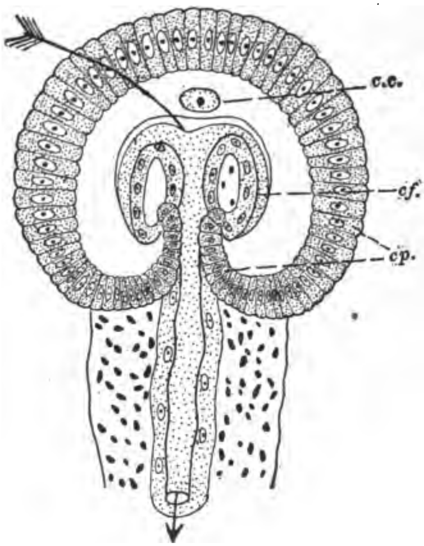


FIG. 89. Nephrostome of the earthworm. *c.c.*, central cell; *cf.*, grooved cells; *cp.*, ciliated marginal cells. (From Dahlgren and Kepner.)

EXCRETION. — A nephridium functions in the following manner. The cilia on the nephrostome and in the thin tube and middle tube create a current through the muscular duct which leads to the exterior. Solid waste particles which may be floating about in the cœlomic fluid are drawn into the nephridium by this current, and pass to the outside. Waste matter in solution is taken from the blood by the glands of the "wide tube" and stored in the large sac-like muscular duct until excreted.

Nervous System. — The nervous system differs from that of *Planaria* and *Ascaris* in being more concentrated. At the an-

terior end of the body in somite III is a bi-lobed mass of nervous tissue (Fig. 90, *2*); this is called the ***brain***, or supra-pharyngeal ganglion, because of its position on the dorsal surface of the pharynx. Two large nerve cords, the *circum-pharyngeal connectives* (*3*), pass around the pharynx one on either side, connecting the brain with a pair of ganglia lying beneath the pharynx in

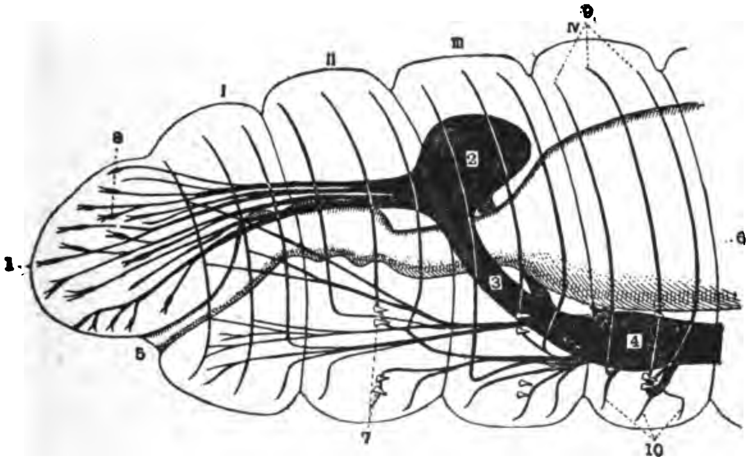


Fig. 90. Diagram of the anterior end of an earthworm to show the arrangement of the nervous system. *1*, prostomium; *2*, brain; *3*, circum-pharyngeal connective; *4*, sub-pharyngeal ganglion; *5*, mouth; *6*, pharynx; *7*, setæ; *8*, tactile nerves to prostomium; *9*, dorsal nerves; *10*, ventral nerves. (From Shipley and MacBride.)

somite IV. These are the *sub-pharyngeal ganglia* (*4*). Every somite posterior to IV contains a ganglionic mass which is connected by a nerve cord with the ganglion in the preceding somite, and also, with the exception of the last, with that in the succeeding somite. This connected row of ganglia is called the ***ventral nerve cord***, and, together with the supra-pharyngeal ganglia, constitutes the *central nervous system.* The nerves which pass from the central nervous system to all parts of the body, and which pass to it from the body wall and internal organs, constitute the

peripheral nervous system (Fig. 90, *9* and *10*). The supra-pharyngeal ganglia supply the prostomium with two large nerves which give off many branches (*8*); they also send nerves into somites II and III. One nerve extends out from each circum-pharyngeal connective. In each somite from IV to the posterior end of the body, three pairs of nerves arise, two pairs from the ganglionic mass and one pair from the sides of the nerve-cord just behind the septum which separates the somite from the one preceding.

Each enlargement of the ventral nerve cord really consists of two ganglia which are closely fused together. In transverse section these fused ganglia are seen to be surrounded by an outer thin layer of epithelium, the peritoneum, and an inner muscular sheath containing blood vessels and connective tissue as well as muscle fibers. Near the dorsal surface are three large areas, each surrounded by a thick double sheath and containing a bundle of nerve fibers. These are called neurochords or "*giant fibers.*" Large pear-shaped *nerve cells* are visible near the periphery in the lateral and ventral parts of the ganglion.

The nerves of the peripheral nervous system are either efferent or afferent. *Efferent* nerve fibers are extensions from cells in the ganglia of the central nervous system. They pass out to the muscles or other organs, and, since impulses sent along them give rise to movements, the cells of which they are a part are said to be *motor nerve cells.* The *afferent* fibers originate from nerve cells in the epidermis which are *sensory* in function, and extend into the ventral nerve cord.

The *functions* of nervous tissue are *perception*, *conduction*, and *stimulation* (89). These are usually performed by nerve cells, called neurons. The *neuron theory* "supposes that there is no nerve fiber independent of nerve cell and that the cell with all its prolongations is a unit or a neuron; that these units are not united to one another anatomically, but act together physiologically by contact; that the entire nervous system consists of superimposed neurons; . . ." (136, p. 633).

The *reflex* carried out either consciously or unconsciously is

considered the physiological unit of nervous activity. The apparatus required for a simple reflex in the body of an earthworm is represented in Figure 91. A primary sensory neuron (*sc.*), lying at the surface of the body, sends a fiber (*sf.*) into the ventral nerve cord where it branches out; these branches are in physiological continuity with branches from a primary motor neuron (*mc.*) lying in the ganglion of the ventral nerve cord. The second

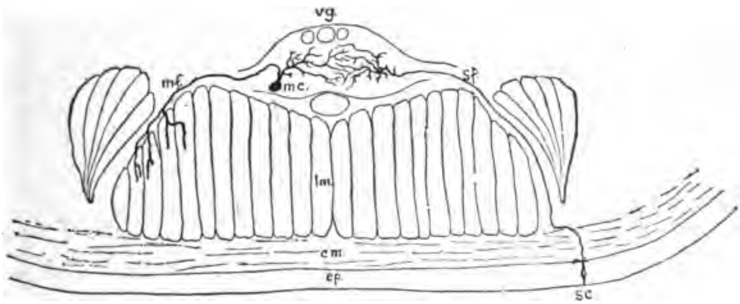


FIG. 91. Transverse section of the ventral nerve chain and surrounding structures of an earthworm. *cm.*, circular muscles; *ep.*, epidermis; *lm.*, longitudinal muscles; *mc.*, motor cell body; *mf.*, motor nerve fiber; *sc.*, sensory cell body; *sf.*, sensory nerve fiber; *vg.*, ventral ganglion. (From Parker in *Pop. Sci. Monthly*, modified after Retzius.)

neuron (*mc.*) sends fibers (*mf.*) into a reacting organ, which in this case is a muscle. These fibers extending to the reacting organ are called motor fibers (*mf.*); those leading to the ventral nerve cord are termed sensory fibers (*sf.*). The first neuron, or *receptor*, receives the stimulus and produces the nerve impulse; the second neuron, the *adjustor*, receives, directs, and modifies the impulse; and the muscle or other organ stimulated to activity is the *effector*. Within the ventral nerve cord are *association neurons* whose fibers serve to connect structures within one ganglion or two succeeding ganglia. These short neurons overlap one another, and are doubtless responsible for the muscular waves which pass from the anterior to the posterior end of the worm during locomotion. The three *giant fibers*, which lie in the dorsal part of

the ventral nerve cord throughout almost its entire length, are connected by means of fibrils with nerve cells in the ganglia and probably distribute the impulse that causes a worm to contract its entire body when strongly stimulated (151).

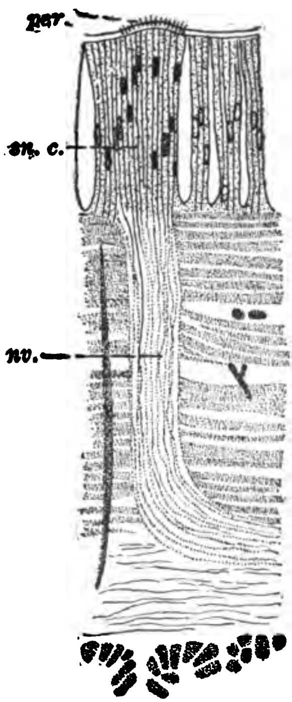


FIG. 92. Tactile nerve endings in the integument of the earthworm. *per.*, sensory hairs projecting through the cuticle; *nv.*, nerve; *sn. c.*, sense cells. (From Dahlgren and Kepner.)

Sense Organs. — The sensitiveness of *Lumbricus* to light and other stimuli is due to the presence of a great number of epidermal sense organs. These are groups of sense cells (Fig. 92, *sn. c.*) connected with the central nervous system by means of nerve fibers (*nv.*), and communicating with the outside world through sense hairs (*per.*) which penetrate the cuticle. More of these sense organs occur at the anterior and posterior ends than in any other region of the body (see Fig. 90, *8*). The epidermis of the earthworm is also supplied with efferent nerve fibers which penetrate between the epidermal cells forming a sub-epidermal network (144, 147).

Reproduction. — FEMALE ORGANS (Fig. 93). — The female reproductive organs are a pair of *ovaries* (*O*) in somite XIII, two *oviducts* (*OD*) in somites XIII and XIV, and two pairs of *seminal receptacles* (*S*) or *spermathecæ* lying in somites IX and X. The ovaries are small pear-shaped bodies. They lie one on either side of the mid-ventral line in somite XIII, and are attached by their larger ends to the ventral part of the anterior septum. The oviducts

consist of the following parts: posterior to each ovary is a *ciliated funnel* which passes through the septum between somites XIII and XIV, enlarges into an *egg sac* (*R*), and then narrows

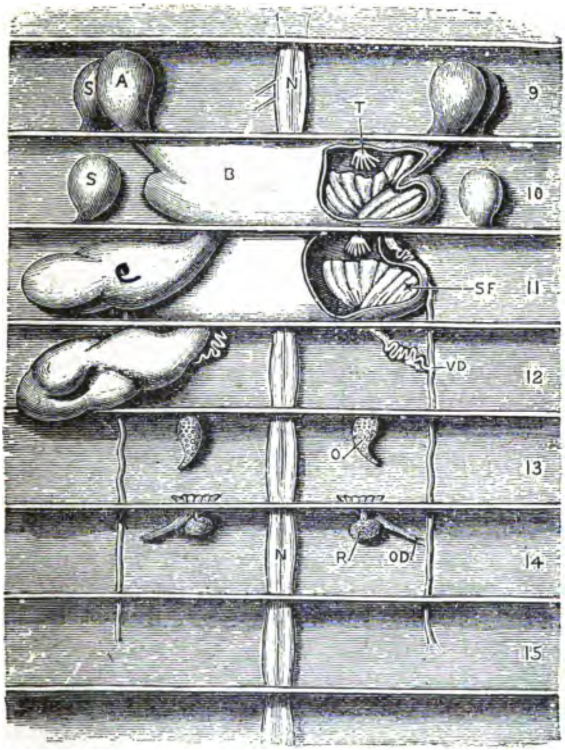


FIG. 93. Diagram of the reproductive organs of the earthworm, dorsal view. *A*, *B*, *C*, seminal vesicles; *N*, nerve cord; *O*, ovary; *OD*, oviduct; *R*, egg sac; *S*, spermatheca; *SF*, seminal funnel; *T*, testes; *VD*, vas deferens. (From Marshall and Hurst.)

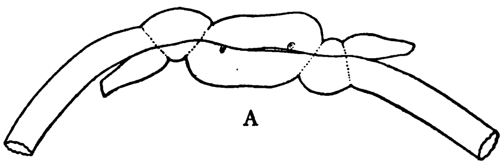
into a *thin duct* (*OD*) which opens to the outside on the ventral surface of the body near the center of somite XIV. The spermathecæ are white globular sacs situated near the ventral body

wall, one pair in somite IX, the other in somite X. They open to the outside through the spermathecal pores between somites IX and X, and X and XI.

Male Organs (Fig. 93). — The male reproductive organs are two pairs of glove-shaped *testes* (*T*), one pair in somite X, the other in somite XI. They occupy positions in the somites similar to that of the ovaries. Behind each testis is a *ciliated funnel* (*SF*) shaped like a rosette; this is the opening of the sperm duct or *vas deferens* (*VD*). This duct passes through the septum just back of the funnel, forms several convolutions, and then extends backward near the ventral surface. The two sperm ducts arising on either side of the mid-ventral line unite in somite XII and then run back as a single tube, opening to the outside through the spermiducal pore on somite XV. In a sexually mature earthworm, the testes and funnel-shaped inner openings of the sperm ducts are inclosed by large white sacs, the *seminal vesicles* (*A*, *B*, *C*), lying in somites IX to XII. There are three pairs of these sperm sacs, one in somite IX (*A*), one in somite XI (*C*), and the third in somite XII. In somites X and XI are central reservoirs (*B*).

Copulation. — Many of the events which precede the laying of eggs by the earthworm have not yet been learned. Reproduction is best known in the common manure worm, *Allolobophora fœtida*. The *breeding season* begins early in the spring and continues until late in the autumn. Sexually mature worms possess a much swollen clitellar region. Although both eggs and sperms are produced by every individual, self-fertilization does not take place, but the eggs of one worm are fertilized by the sperm of another. The sperm are transferred from one worm to another during a process called copulation, which usually takes place just beneath the surface of the earth. Two worms come together with their heads in opposite directions, and their ventral surfaces opposed, as shown in Figure 94, A. Each secretes about itself a tube of slime which extends from about the eighth to the thirty-sixth somite. Four bandlike thickenings, probably of the slime

tubes, encircle both worms at the anterior and posterior edges of the clitellar regions. These hold the worms firmly together and may later aid in closing the ends of the cocoons. The slime tube protects the cocoon as it develops, and confines the seminal fluid and spermatophores. During copulation sperms are not exchanged between the spermathecæ of the two worms, but the spermathecæ of each are loaded from the spermaducal pore of the other, or spermatophores formed in the spermathecæ of one individual are attached to the skin of the other.



COCOONS. — Cocoons are formed either during copulation, or after the two worms have separated. In the former case a band is secreted about the clitellar region of one worm and three or more opposite somites of the other worm. At first the cocoons are perfectly white (Fig. 94, B), but after deposition the exposure to the air changes them to a yellow color. When copulation is completed, the worms slowly withdraw backward from the slime tube and cocoon. As the cocoon is slipped over the head, its ends contract, forming a turnip-shaped capsule, lying within the slime tube (Fig. 94, B). The cocoon after deposition contains, on an average, four eggs, each of which has been penetrated by from one to as many as nine spermatozoa. The nucleus of a single spermatozoon unites with the egg nucleus; the remaining spermatozoa disintegrate (141, 142).

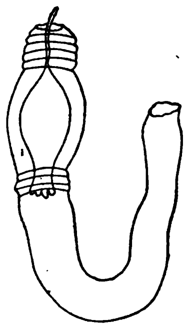


FIG. 94. A, the anterior segments of two copulating earthworms. Slime tubes encircle the pair from the 8th to the 33d segment. B, cocoon, freshly deposited, of an earthworm surrounded by one half of a slime tube. (After Foot in *Journ. Morph.*)

Before considering the embryology of the earthworm, the development of the eggs and spermatozoa and the history of these previous to fertilization must be described.

SPERMATOGENESIS. — During the development of the spermatozoa, the primordial germ cells separate from the testes, and lie in the cavities of the seminal vesicles. The nucleus of each germ cell divides into 2, 4, 8, or 16 daughter nuclei, which become arranged in a single layer near the surface of the cell. Cell walls now appear, extending inward from the periphery, the result being a colony of cells attached by cytoplasmic pedestals to a central non-nucleated mass. The cells of the colony then divide, increasing the number to 32, 64, 128 or more. A dissociation of the colony into several parts now takes place, each part containing a number of spermatogonia. Such a spermatogonial group finally becomes a spherical morula of 32 primary spermatocytes, which are still fastened by cytoplasmic threads to a central body called the *blastophore*. Each group of primary spermatocytes gives rise to 64 secondary spermatocytes, and these divide to form 128 spermatids. The latter then metamorphose into spermatozoa. The number of chromosomes in the spermatozoa is sixteen; this is one half the number contained in the somatic cells, the reduction having taken place during maturation by the union of the chromosomes two by two in the secondary spermatocytes, and a subsequent separation when the spermatids were formed (138, 140).

During the later stages of copulation the spermatozoa are drawn into the rosette-like funnels (Fig. 93, *SF*) of the *vas adeferentia*, pass through these ducts, and are transferred to the spermathecæ of the other worm. Here they are stored until the cocoon passes over the openings of the spermathecæ during the withdrawal of the worm, when some of them pass into the nutrient fluid which has been secreted into the cavity of the cocoon.

OOGENESIS. — The eggs develop in the ovaries (Fig. 93, *O*). These are pear-shaped bodies composed of egg cells in various stages of growth. The basal portion of each ovary consists of

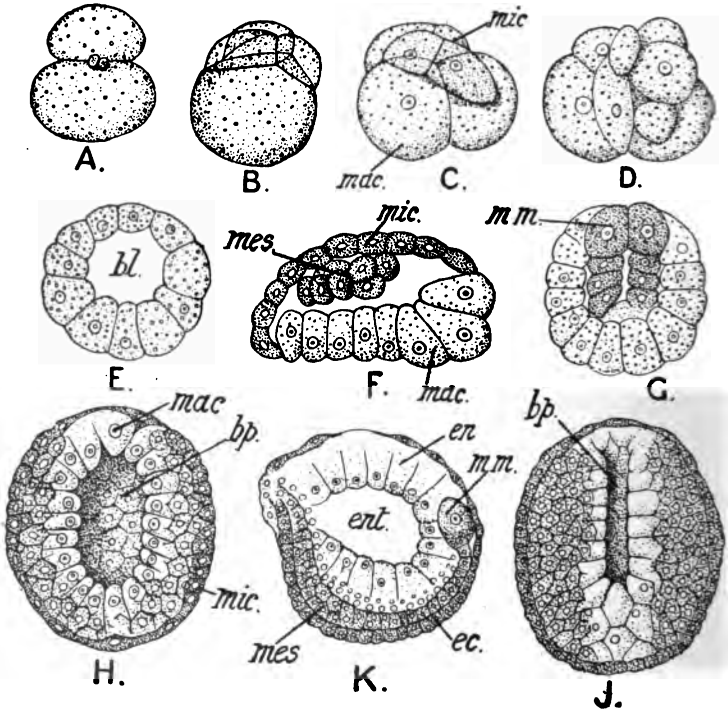


FIG. 95. Stages in the embryology of the earthworm. A, two-celled stage; B, four-celled stage; C, six-celled stage; D, eight-celled stage; E, blastula in section; F, blastula flattened; G, stage showing mesoblastic bands; H, gastrula; J, older gastrula; K, longitudinal section of later stage. *bl.*, blastocœl; *bp.*, blastopore; *ec.*, ectoderm; *en.*, entoderm; *mac.*, macromere; *mes.*, mesoderm; *mic.*, micromere; *mm.*, mesomeres. (From Bourne after Wilson.)

primitive germ cells; from here to the pointed end of the ovary the cells increase in size, those toward the extreme end being recognizable as eggs, each of which is surrounded by a follicle of small nutritive cells. Eggs separate from the end of the ovaries and pass into the body cavity. From here they enter the ciliated funnel of the oviduct, thence into the egg sac (Fig. 93, *R*), where part of the maturation processes occur. From here they either pass out into the cavity of the slime tube and are conveyed from the external openings of the oviduct on somite XIV to the cocoon, or enter the cocoon when it passes over this somite during deposition (142).

FERTILIZATION. — The eggs are penetrated by spermatozoa after the cocoon is shed. At this time they have not completed their maturation processes (141, 142).

Embryology. — The eggs of the earthworm are *holoblastic*, but *cleavage* is unequal, the first division resulting in one large and one small cell (Fig. 95, A). The second cleavage divides the small cell into two equal parts and cuts off a small cell from the larger (B). Because of their difference in size, the large cells are called *macromeres* (*mac.*) and the small cells, *micromeres* (*mic.*). Cleavage becomes irregular after the second division. Both the macromeres and micromeres continue to divide, the number of cells increasing to six (C), eight (D), etc. Soon a cavity, the *blastocœl* (*bl.*), appears between the micromeres and macromeres, and a hollow sphere recognizable as a *blastula* results (E). Two of the larger cells of the blastula lying side by side behave differently from the others. They project down into the blastocœl, and, by repeated divisions, give rise to two rows of small cells (*mes.* and *mm.* in F and G). Because of the fact that these two cells give rise to the mesoderm, they are termed *mesomeres*, and the two rows of cells derived from them, the *mesoblastic bands*. While the mesomeres are dividing, the blastula becomes flattened (F), the larger cells form a plate of clear columnar cells (*mac.*), and the small cells spread out into a thin dome-shaped epithelium (*mic.*).

Bilateral symmetry is already established at this early period; the mesoblastic bands lie along what will become the longitudinal axis of the future worm, and the mesomeres occupy the posterior end. A *gastrula* is now formed by the invagination of the plate of large cells (H); the edges of the cavity thus produced fold in until only a slit remains (J). This slit is the *blastopore* (*bp.*), and the cavity is the *enteron*, which later becomes part of the alimentary canal. Soon the slit closes, except at one end where a pore, the future *mouth*, remains. The three germ layers are at this time quite distinct, and are well shown in a longitudinal section of the gastrula (K). The large clear cells which invaginated line the enteron, becoming the *entoderm* (*en.*); the dome-shaped epithelium of small cells covers the outer surface and represents the *ectoderm* (*ec.*); and between these two layers are the two rows of mesoblastic bands which give rise to the *mesoderm* (*mes.*) (157).

The detailed history of these *germ layers* is too long and complicated to be discussed in a book of this character. The development of the mesodermal layers and cœlom should, however, be mentioned. The mesoderm becomes separated into two layers between which a cavity, the *cœlom*, is formed. The outer layer, called the *somatopleure*, clings to the ectoderm, and gives rise to the muscles of the body wall; the inner layer, called the *splanchnopleure*, remains attached to the enteron and gives rise to the muscles of the alimentary canal. All other structures of mesodermal origin are derived from these two layers. After the establishment of the germ layers as described above, the embryo elongates, and finally becomes vermiform, escaping from the cocoon in about two or three weeks.

Behavior. — EXTERNAL STIMULI. — The external stimuli that have been most frequently employed in studying the behavior of earthworms are those dealing with thigmotropism, chemotropism, and phototropism (135, 145, 150, 152, 153, 155, 156).

THIGMOTROPISM. — Mechanical stimulation, if continuous and not too strong, calls forth a positive reaction; the worms live

where their bodies come in contact with solid objects; they apparently like to feel the walls of their burrows against their bodies or, when outside of their burrows, to lie or crawl upon the ground (155). Reactions to sounds are not due to the presence of a sense of hearing, but to the contact stimuli produced by vibrations. Darwin showed that musical tones produced no response, but that the worms contained in a flower pot drew back into their burrows immediately when a note was struck, if the pot were placed upon a piano, this result being due to vibrations.

CHEMOTROPISM. — Contact is not sufficient to cause burrowing, but a combination of mechanical and chemical stimuli seems necessary — at least this is true of the small earthworm, *Allolobophora fœtida*, found in heaps of manure. A worm of this species does not burrow when placed in contact with dry filter paper; but immediately responds if the paper is wet with water or liquid taken from manure. In certain cases chemotropic reactions result in bringing the animal into regions of favorable food conditions, or turning it away from unpleasant substances. Moisture, which is necessary for respiration and consequently for the life of the earthworm, causes a positive reaction, provided it comes in contact with the body, — no positive reactions being produced by chemical stimulation from a distance. Negative reactions, on the other hand, such as moving to one side or back into the burrow, are produced even when certain unpleasant chemical agents are still some distance from the body. These reactions are quite similar to those caused by contact stimuli. Darwin explained the preference of the earthworm for certain kinds of food by supposing that the discrimination of edible from inedible substance was possible when in contact with the body. This would resemble the sense of taste as present in the higher animals. Such a sense might account also for the positive burrowing reaction cited above, which is caused by contact with fluids from manure.

Certain experiments in which animals were subjected to solutions of sodium, ammonium, lithium, and potassium chlorides

seem to show that the worms are stimulated in different degrees by them, since the interval of time between the application of the stimulus and the reaction differs for each substance, being shorter for sodium chloride, and successively longer for the others in the order named (153). In man these substances all taste practically alike, because of the presence of chlorine.

Phototropism. — No definite visual organs have been discovered in earthworms, but nevertheless these animals are very sensitive to light, as is proved by the fact that a sudden illumination at night will often cause them to "dash like a rabbit" into their burrows. One investigator claims to have found cells in the ectoderm, especially in the prostomium and posterior end, which act as visual organs (144). The entire surface of the body, however, is sensitive to light, although the anterior region is more sensitive than the tail, and the middle less than either of the others. If an animal, which is lying along the ground with its tail clinging to the top of the burrow, is suddenly illuminated, it promptly withdraws into its hole; if not in touch with its burrow, it will crawl away from the source of light. Very slight differences in the intensity of the light are distinguished, since, if a choice of two illuminated regions is given, that more faintly lighted is, in the majority of cases, selected. Thus far we have considered light as causing a negative response; but a positive reaction to faint light has been demonstrated for *Allolobophora fœtida* (135). This positive phototropism to faint light may account for the emergence of the worms from their burrows at night. Experiments with lights of different colors show that red is preferred to any other, green being next, and blue last, and that the intensity of the colored rays determines the effect (156).

Combinations and Interference of Stimuli. — It has been shown that contact and chemical stimuli may combine, as in the case of the burrowing reaction of *Allolobophora fœtida*. In other instances stimuli interfere with one another; for example, light calls forth no reaction if the animals are feeding or mating.

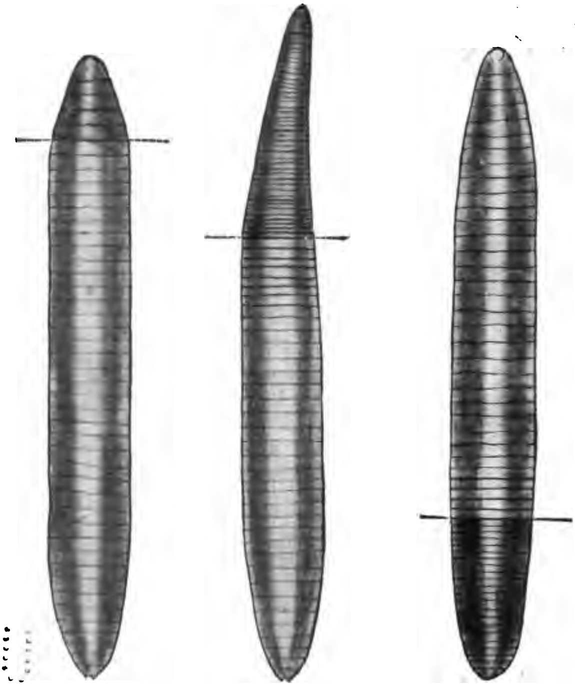


FIG. 96. Regeneration in the earthworm. A, head end of five segments regenerated from the posterior piece of a worm; B, tail regenerated from the posterior piece of a worm; C, tail regenerated from an anterior piece of a worm. (From Morgan.)

Physiological State. — From the foregoing account it might be inferred that only external stimuli are factors in the behavior of the earthworm. This, however, is not the case, since the physiological condition, which depends largely upon previous stimulation, determines the character of the response. Different physiological states may be recognized, ranging from a state of rest in which slight stimuli are not effective, to a state of great excitement caused by long-continued and intense stimulation, in which condition slight stimuli cause violent responses (145).

Regeneration. — A general account of this phenomenon has already been given on pages 138–139, and this should be read in order that the following paragraphs may be perfectly clear. If the anterior portion of an earthworm is cut off at any point between the end of the prostomium and the fifteenth to the eighteenth segment, a new anterior end will grow out from the cut end of the body. The piece regenerated will consist of one segment, if only one segment is removed; of two segments, if two segments are removed; of three, four, or five segments, if three, four, or five segments are removed; but never more than segments I to V are regenerated, regardless of the number removed (Fig. 96, A), and no new reproductive organs appear if the original ones were contained in the severed piece. If the cut is made behind segment XVIII, a tail will grow out from the cut surface of the posterior piece, producing a worm consisting of two tails joined at the center (Fig. 96, B). Such a creature cannot take in food, and must slowly starve to death. When the regenerated part is different from the part removed, as in the case just cited, the term *heteromorphosis* is given to the phenomenon.

If the posterior portion of an earthworm is cut off at any point between the anal segment and the twelfth to the fifteenth segment, a new tail will grow out from the cut surface of the part remaining (Fig. 96, C). Regeneration of a tail differs from that of a head, since more than five segments are replaced. The anal segment develops first, and then a number of new segments are introduced between it and the old tissue.

The rate of regenerative growth depends upon the amount of old tissue removed. Thus, if only a few segments of the posterior end are cut off, a new tail regenerates very slowly; if more is removed, the new tissue is added more rapidly. In fact, the rate of growth increases up to a certain point as the amount removed increases. The factors regulating the rate of regeneration have not yet been fully determined, although several possible explanations have been suggested.

Grafting. — Pieces of earthworms may be grafted upon other worms without much difficulty. Several results are shown in Figure 97. Three pieces may be so united as to produce a very long worm (A); the tail of one animal may be grafted upon the side of another, producing a double-tailed worm (B); or the anterior end of one individual may be united with that of another (C). In all these experiments the parts were held together by threads until they became united.

2. Annelids in General

The two chief classes of Annelids are the Chætopoda or Earthworms and marine Annelids, and the Hirudinea or Leeches. Class Chætopoda may be divided into two subclasses, the Oligochæta, to which the earthworm belongs, and the Polychæta. Table VI contrasts the characters of these two divisions, and Figure 98 shows one of the most common Polychæts, the marine annelid, *Nereis*.

The members of the Class Hirudinea have neither setæ nor parapodia. They move by means of a ventral sucker near the posterior end, and a sucker mouth on the ventral surface at the anterior end. They are flattened dorso-ventrally. The grooves on the outside of the body do not correspond in number or position to the septa within, there being several external rings to each internal segment. The cœlom is not as large as in the Chætopods, being reduced to the cavities in which the germ cells lie, and a

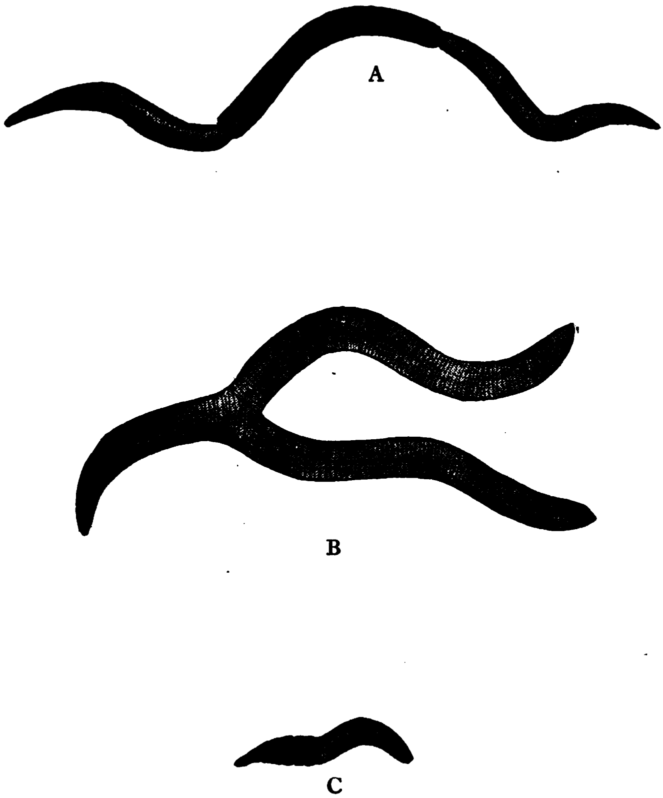


FIG. 97. Grafting in the earthworm. A, union of three pieces to make a long worm; B, union of two pieces to make a double-tailed worm; C, anterior and posterior pieces united to make a short worm. (From Morgan.)

number of small spaces. Leeches are usually aquatic, hermaphrodite, and have a direct development. Figure 99 shows a common representative of this class.

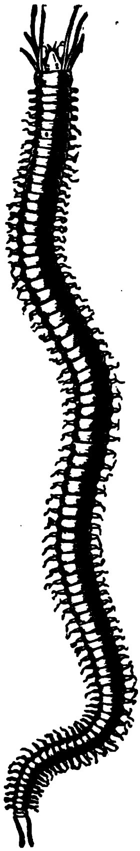


FIG. 98. A marine Polychæt, *Nereis*. (From Shipley and MacBride, after Oersted.)

FIG. 99. A leech, *Hirudo medicinalis*. 1, mouth; 2, posterior sucker; 3, sensory papillæ. (From Shipley and MacBride.)

TABLE VI

THE CHARACTERS OF OLIGOCHÆTS AND POLYCHÆTS CONTRASTED

OLIGOCHÆTA	POLYCHÆTA
No special locomotor protrusions (parapodia); few setæ.	Parapodia; many setæ.
No other external appendages.	External appendages in the form of antennæ, gills, and cirri (see Fig. 98).
Hermaphrodite.	Sexes usually separate.
Development direct.	A metamorphosis in development.
Aquatic (fresh-water) or terrestrial.	Aquatic (marine).

CHAPTER XI

THE CRAYFISH AND ARTHROPODS IN GENERAL

1. THE CRAYFISH

(*Cambarus virilis* Girard)[1]

CRAYFISHES inhabit fresh-water lakes, ponds, and streams. The species *Cambarus virilis* is common in some of the central states and *Cambarus affinis* in the eastern part of the country. The lobster is so nearly like the crayfish in structure that the anatomical portion of this chapter may be applied also in large part to this animal. In Europe the most common crayfish is *Astacus fluviatilis*, a species made famous by Huxley's classical work "The Crayfish."

The crayfish, *Cambarus virilis*, is usually found concealed under rocks or logs at the bottom of ponds and streams. Here it lies with its head toward the entrance to its hiding place. When crawling about or swimming in the open water, its hard shell helps protect it from fish, while its color, which resembles the bottom, tends to make its detection difficult. Crayfishes may be captured easily by hand, with a net, or by fishing for them with a string baited with a piece of meat. They thrive in an aquarium, and their entire life history may be observed in the laboratory. The yearly decrease in the number of lobsters available for food,

[1] The complete life history, and the details of the anatomy are not known for any single species of the genus *Cambarus*. The following account, therefore, must necessarily be a composite containing not only observations on various species of *Cambarus*, but also on the European crayfish, *Astacus (Potamobius) fluviatilis*. The differences between these crayfishes are, however, so slight as to be of little importance except in a detailed monograph.

and the steadily increasing demand for crayfishes, will undoubtedly soon make it worth while to raise the latter for market (162).

External Features. — EXOSKELETON. — The outside of the body of the crayfish is covered by an extremely hard chitinous ***cuticle*** impregnated with lime salts. This exoskeleton is thinner and flexible at the joints, allowing movement. A delicate cuticle of the same substance (chitin) was noted in the earthworm (p. 166).

REGIONS OF THE BODY. — Unlike the earthworm, the body of the crayfish shows two distinct regions, an anterior rigid portion, the *cephalothorax*, and a posterior series of segments, the ***abdomen.***

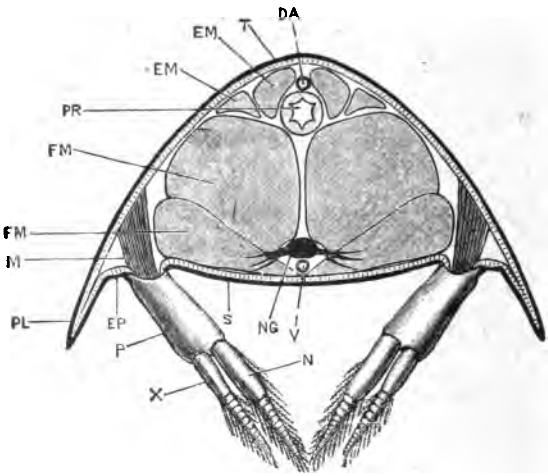


FIG. 100. Transverse section through the abdomen of the crayfish. *DA*, dorsal abdominal artery; *EM*, extensor muscles of the abdomen; *EP*, epimeron; *FM*, flexor muscles of abdomen; *M*, muscles of appendage; *N*, endopodite; *NG*, nerve ganglion; *P*, protopodite; *PL.* pleuron; *PR*, intestine; *S*, sternum; *T*, tergum; *V*, ventral abdominal artery; *X*, exopodite. (From Marshall and Hurst.)

The entire body is segmented, but the joints have been obliterated on the dorsal surface of the cephalothorax.

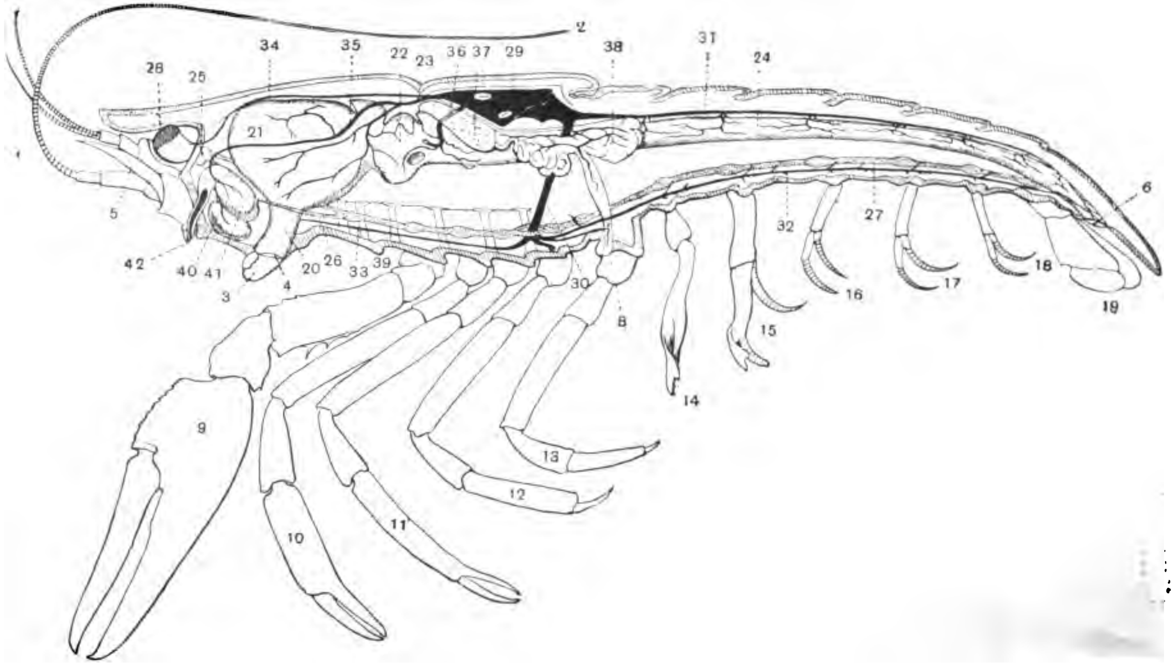


FIG. 101. Semi-diagrammatic view of internal organs and appendages of right side of a male crayfish. *1*, antennule; *2*, antenna; *3*, mandible; *4*, mouth; *5*, exopodite of antenna; *6*, anus; *7*, telson; *8*, opening of vas deferens; *9*, pincher; *10–13*, walking legs; *14–19*, abdominal appendages; *20*, œsophagus; *21*, cardiac chamber of stomach; *22*, pyloric chamber of stomach; *23*, cervical groove; *24*, intestine; *25*, brain; *26*, circum-œsophageal connectives; *27*, ventral nerve cord; *28*, eye; *29*, heart; *30*, sternal artery; *31*, dorsal abdominal artery; *32*, ventral abdominal artery; *33*, ventral thoracic artery; *34*, ophthalmic artery; *35*, antennary artery; *36*, hepatic artery; *37*, testis; *38*, vas deferens; *39*, internal skeleton; *40*, green gland; *41*, bladder; [illegible]

STRUCTURE OF A SEGMENT. — A typical segment is shown in cross section in Figure 100. It consists of the following parts: (1) a convex dorsal plate, the *tergum* (*T*), (2) a ventral transverse bar, the *sternum* (*S*), (3) plates projecting down at the sides, the *pleura* (*PL*), and (4) smaller plates between the pleura and the basis of the limb, the *epimera* (*EP*).

CEPHALOTHORAX. — The cephalothorax consists of segments I–XIII, which are inclosed dorsally and laterally by a cuticular shield, the *carapace.* An indentation, termed the *cervical groove,* runs across the mid-dorsal region of the carapace, and obliquely forward on either side, separating the *cephalic* or head region from the posterior *thoracic* portion. The anterior pointed extension of the carapace is known as the *rostrum.* Beneath this on either side is an *eye* at the end of a movable peduncle. The *mouth* is situated on the ventral surface near the posterior end of the head region. It is partly obscured by the neighboring appendages. The carapace of the thorax is separated by *branchio-cardiac grooves* into three parts, a median dorsal longitudinal strip, the *areola,* and two large convex flaps, one on either side, the *branchiostegites,* which protect the gills beneath them.

ABDOMEN. — In the abdomen there are six segments, and a terminal extension, the *telson,* bearing on its ventral surface the longitudinal anal opening. Whether or not the telson is a true segment is still in dispute; we shall adopt the view that it is not. The first abdominal segment (XIV) is smaller than the others and lacks the pleuræ. Segments XV–XIX are like the type described above.

APPENDAGES. — With the possible exception of the first abdominal segment in the female, every segment of the body bears a pair of jointed appendages. These are all variations of a common type (Fig. 100), consisting of a basal segment, the *protopodite* (*P*), which bears two branches, an inner *endopodite* (*N*), and an outer *exopodite* (*X*). Beginning at the anterior end, the appendages are arranged as follows (Fig. 101). In front of the mouth are (I) the *antennules,* and (II) the *antennæ;* the mouth

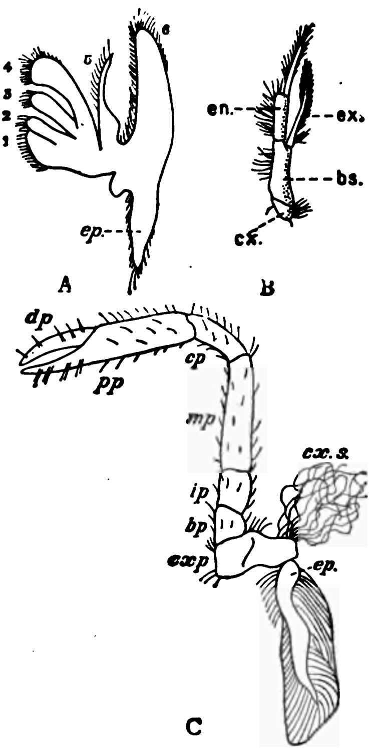


FIG. 102. Types of crayfish appendages. A, second maxilla, foliaceous type; *1–4*, basopodite; *5*, endopodite; *6*, exopodite; *ep.*, scaphognathite. (From Cambridge Natural History.) B, swimmeret, biramous type; *cx. bs.*, protopodite; *ex.*, exopodite; *en.*, endopodite. (From Lankester's Treatise.) C, second walking leg, uniramous type; *cxp. bp.*, protopodite; *ip.*, *mp.*, *cp.*, *pp.*, *dp.*, segments of endopodite; *ep.*, epipodite. (From Cambridge Natural History.)

possesses (III) a pair of *mandibles*, behind which are (IV) the first, and (V) the second *maxillæ;* the thoracic region bears (VI) the first, (VII) the second, and (VIII) the third *maxillipedes*, (IX) the *pinchers* or *chelipeds*, and (X–XIII) four other pairs of *walking legs;* beneath the abdomen are six (XIV–XIX) pairs of *swimmerets*, some of which are much modified. Table VII gives brief descriptions of the different appendages, and shows the modifications due to differences in function. The functions of some of the appendages are still in doubt.

Three kinds of appendages can be distinguished in the adult crayfish; (1) the *foliaceous*, *e.g.* the second maxilla (Fig. 102, A), (2) the *biramous*, *e.g.* the swimmerets (Fig. 102, B), and (3) the *uniramous*, *e.g.* the walking legs (Fig. 102, C). All of these appendages have doubtless been derived from a single type, the modifications being due to the functions performed by them. The biramous type probably

TABLE VII

DESCRIPTIVE TABLE OF THE APPENDAGES OF THE CRAYFISH

Appendage	Protopodite	Exopodite	Endopodite	Function
I. Antennule	3 segments; statocyst in basal segment	Many-jointed filament	Many-jointed filament	Tactile; chemical; equilibration
II. Antenna	2 segments; excretory pore in basal segment	Broad, thin, dagger-like lateral projection	A long many-jointed "feeler"	Tactile; chemical.
III. Mandible	2 segments; a heavy jaw and basal segment of palp	Absent	Small; 2 distal segments of palp	Crushing food
IV. 1st Maxilla	2 thin lamellæ extending inward	Absent	A small outer lamella	
V. 2d Maxilla	2 bilobed lamellæ	Dorsal half of plate, the scaphognathite	1 segment; small, pointed	Creates current of water in gill chamber
VI. 1st Maxilliped	2 thin segments extending inward; a broad plate, the epipodite extending outward	A long basal segment bearing a many-jointed filament	Small; 2 segments	Chemical; tactile; holds food
VII. 2d Maxilliped	2 segments; a basal coxopodite bearing a gill, and a basipodite bearing the exopodite and endopodite	Similar to VI	5 segments; the basal one long and fused with the basipodite	Similar to VI

TABLE VII (*Continued*)

DESCRIPTIVE TABLE OF THE APPENDAGES OF THE CRAYFISH

Appendage	Protopodite	Exopodite	Endopodite	Function
VIII. 3d Maxilliped	Similar to VII	Similar to VI	Similar to VII, but larger	Similar to VI
IX. 1st Walking Leg (Chela, Cheliped, or Pincher)	2 segments; coxopodite, and basipodite	Absent	5 segments, the terminal two forming a powerful pincher	Offense and defense; aids in walking; tactile
X. 2d Walking Leg (Pareiopod)	Similar to IX	Absent	As in IX, but not so heavy	Walking; prehension; toilet implements
XI. 3d Walking Leg	Similar to IX; coxopodite of female contains genital pore	Absent	Similar to X	Similar to X
XII. 4th Walking Leg	Similar to IX	Absent	Similar to X, but no pincher at end	Walking
XIII. 5th Walking Leg	Similar to IX; coxopodite of male bears genital pore	Absent	Similar to XII	Walking; cleaning abdomen and eggs
XIV. 1st Abdominal (1st Pleopod or Swimmeret)				Reduced in female; in male, protopodite and endopodite fused together forming an organ for transferring sperm.

XV. 2d Abdominal (2d Pleopod or Swimmeret)	In female 2 segments	In female many-jointed filament	In female like exopodite but longer	In female as in XVI; in male modified for transferring sperm to female
XVI. 3d Abdominal (3d Pleopod or Swimmeret)	2 segments	Many-jointed filament	Like exopodite but longer	Creates current of water; in female used for attachment of eggs and young
XVII. 4th Abdominal (4th Pleopod or Swimmeret)	2 segments	As in XVI	As in XVI	As in XVI
XVIII. 5th Abdominal (5th Pleopod or Swimmeret)	As in XVII	As in XVI	As in XVI	As in XVI
XIX. 6th Abdominal (Uropod)	1 short, broad segment	Flat oval plate divided by transverse groove into two parts	Flat oval plate	Swimming

represents the condition from which the other types developed. The uniramous walking legs, for example, pass through a biramous stage during their embryological development. Again, the biramous embryonic maxillipedes are converted into the foliaceous type by the expansion of their basal segments (166).

General Internal Anatomy. — The body of the crayfish contains all of the important systems of organs characteristic of the higher animals. The cœlom is not a large cavity, as in the earthworm, but is restricted to the cavities of the reproductive organs. Certain of the organs are metamerically arranged, *e.g.* the *nervous system;* others like the *excretory organs,* are concentrated into a small space. The systems of organs and their functions will be presented in the following order: (1) digestive, (2) vascular, (3) respiratory, (4) excretory, (5) nervous, (6) sense organs, (7) muscular, and (8) reproductive.

Digestive System. — The alimentary canal of *Cambarus* consists of the following parts (Fig. 101): —

(1) The *mouth* (*4*) opens on the ventral surface between the jaws (*3*).

(2) The *œsophagus* (*20*) is a short tube leading from the mouth to the stomach.

(3) The *stomach* is a large cavity divided by a constriction into an anterior *cardiac* chamber (*21*) and a smaller posterior *pyloric* chamber (*22*). In the stomach are a number of chitinous ossicles of use in chewing the food, and collectively known as the *gastric mill.* The most important of these are (*a*) a median cardiac ossicle, (*b*) a median urocardiac ossicle, (*c*) two lateral pterocardiac ossicles, (*d*) a pair of lateral zygocardiac ossicles, (*e*) a pyloric ossicle, and (*f*) a prepyloric ossicle. The ossicles are able to move one upon another, and, being connected with powerful muscles, are effective in grinding up the food. On either side of the pyloric chamber enters a duct of the digestive glands, and above is the opening of the small cæcum.

At certain times two calcareous bodies, known as *gastroliths,* are present in the lateral walls of the cardiac chamber of the

stomach. Their function is not certain, but is probably for the storage of the calcareous matter used in hardening the exoskeleton.

(4) The *intestine* (*24*) is a small tube passing posteriorly near the dorsal wall of the abdomen, and opening to the outside through the *anus* (*6*) on the ventral surface of the telson (*7*).

The *digestive glands*, or "liver," are situated in the thorax, one on either side. Each consists of three lobes composed of a great number of small tubules. The glandular epithelium lining these tubules produces a secretion which passes into the *hepatic ducts* and thence into the pyloric chamber of the stomach.

Nutrition. — FOOD. — The food of the crayfish is made up principally of living animals such as snails, tadpoles, insect larvæ, small fish, and frogs; but decaying organic matter is also eaten. Not infrequently crayfishes prey upon others of their kind. They feed at night, being more active at dusk and daybreak than at any other time (167). Their method of feeding may be observed in the laboratory if a little fresh meat is offered to them. The maxillipedes and maxillæ hold the food while it is being crushed into small pieces by the mandibles. It then passes through the œsophagus into the stomach. The coarser parts are ejected through the mouth.

DIGESTION. — In the cardiac chamber of the stomach, the food is ground up by the ossicles of the gastric mill. When fine enough, it passes through the *strainer* which lies between the two divisions of the stomach. This strainer consists of two lateral and a median ventral fold which bear hairlike setæ, and allow the passage of only liquids or very fine particles. In the pyloric chamber, the food is mixed with the secretion from the digestive glands brought in by way of the hepatic ducts. From the pyloric chamber the dissolved food passes into the intestine by the walls of which the nutritive fluids are absorbed. Undigested particles pass on into the posterior end of the intestine, where they are gathered together into fæces, and egested through the anus.

Vascular System. — THE BLOOD. — The blood into which the absorbed food passes is an almost colorless liquid in which are

suspended a number of ameboid cells, the *blood corpuscles* or amebocytes. The principal *functions* of the blood are the transportation of food materials from one part of the body to another, of oxygen from the gills to the various tissues, of carbon dioxide to the gills, and of urea to the excretory organs. If a crayfish is wounded, the blood, on coming in contact with the air, thickens, forming a clot. It is said to *coagulate*. This clogs the opening and prevents loss of blood. The chelipeds and other walking legs of the crayfish have a breaking point near their bases. When one is injured the animal may break the limb at this point and lessen the blood flow, since only a small space is present in the appendage at this particular spot, and coagulation, therefore, takes place very quickly.

BLOOD VESSELS. — The principal blood vessels are a heart, seven main arteries, and a number of spaces called sinuses.

HEART. — The *heart* (Fig. 101, *29*) is a muscular-walled, saddle-shaped sac lying in the *pericardial sinus* in the median dorsal part of the thorax. It may be considered as a dilatation of a dorsal vessel resembling that of the earthworm. Six elastic *ligaments*, two anterior, two posterior, and two running along the ventral border of each lateral surface, fasten it to the walls of the pericardial sinus. Three pairs of valvular apertures, called *ostia*, one dorsal and two lateral, allow the blood to enter from the surrounding sinus (174).

ARTERIES. — Five arteries arise from the anterior end of the heart (Fig. 101).

(1) The *ophthalmic* artery (*34*) is a median dorsal tube passing forward over the stomach, and supplying the cardiac portion, the œsophagus, and head.

(2, 3) The two *antennary* arteries (*35*) arise one on each side of the ophthalmic artery, pass forwards, outwards, and downwards, and branch, sending a gastric artery to the cardiac part of the stomach, arteries to the antennæ, to the excretory organs, and to the muscles and other cephalic tissues.

(4, 5) The two *hepatic* arteries (*36*) leave the heart below

the antennary arteries. They lead directly to the digestive glands.

A single dorsal abdominal artery arises from the posterior end of the heart.

(6) The *dorsal abdominal artery* (*31*) is a median tube leading backwards from the ventral part of the heart, and supplying the dorsal region of the abdomen. It branches near its point of origin, giving rise to the sternal artery (*30*); this leads directly downward, and, passing between the nerve cords connecting the fourth and fifth pairs of thoracic ganglia (see p. 205) divides into two arteries. One of these, the *ventral thoracic* artery, runs forward beneath the nerve chain, and sends branches to the ventral thoracic region, and to appendages III to XIII; the other, the *ventral abdominal* artery (*32*), runs backward beneath the nerve chain, and sends branches to the ventral abdominal region and to the abdominal appendages.

SINUSES. — The blood passes from the arteries into spaces lying in the midst of the tissues, called sinuses. The pericardial sinus has already been mentioned. The thorax contains a large ventral blood space, the *sternal sinus*, and a number of *branchio-cardiac canals* extending from the bases of the gills to the pericardial sinus. A *perivisceral sinus* surrounds the alimentary canal in the *cephalothorax*.

BLOOD FLOW.—The heart, by means of rhythmical contractions, forces the blood through the arteries to all parts of the body. Valves are present in every artery where it leaves the heart; they prevent the blood from flowing back. The finest branches of these arteries, the *capillaries*, open into spaces between the tissues, and the blood eventually reaches the sternal sinus. From here it passes into the *efferent channels* of the gills and into the gill filaments, where the carbonic acid in solution is exchanged for oxygen from the water in the branchial chambers. It then returns by way of the *afferent gill channels*, passes into the branchio-cardiac sinuses, thence to the pericardial sinus, and finally through the ostia into the heart. The valves of the ostia allow

the blood to enter the heart, but prevent it from flowing back into the pericardial sinus.

Respiratory System. — Between the branchiostegites and the body wall are the branchial chambers containing the gills. At the anterior end of the branchial chamber is a channel in which the *scaphognathite* of the second maxilla (Fig. 102, *A*, *ep.*) moves back and forth, forcing the water out through the anterior opening. Water flows in through the posterior opening of the branchial chamber.

GILLS. — There are two rows of gills, named according to their points of attachment. The outermost, the *podobranchiæ*, are fastened to the coxopodites of certain appendages (see Table VIII) and the inner double row, the *arthrobranchiæ*, arise from the membranes at the bases of these appendages. In *Astacus* there is a third row, the *pleurobranchiæ*, attached to the walls of the thorax. The number and arrangement of these gills are shown in Table VIII (169). The podobranchiæ consist of a

TABLE VIII

THE NUMBER AND POSITION OF THE GILLS OF THE CRAYFISH
(*Cambarus*)

SEGMENT	PODOBRANCHIÆ	ARTHROBRANCHIÆ		TOTAL NUMBER
		Anterior	*Posterior*	
VI	0 (*ep.*)	0	0	0 (*ep.*)
VII	1	1	0	2
VIII	1	1	1	3
IX	1	1	1	3
X	1	1	1	3
XI	1	1	1	3
XII	1	1	1	3
	6 (*ep*).	6	5	17 (*ep.*)

basal plate covered with delicate setæ and a central axis bearing a thin, longitudinally folded corrugated plate on its distal end, and a feather-like group of *branchial filaments*. The arthrobranchiæ have a central stem on either side of which extends a number of filaments, causing the entire structure to resemble a plume.

Attached to the base of the first maxilliped is a broad thin plate, the *epipodite*, which has lost its branchial filaments.

Excretory System. — The excretory organs are a pair of rather large bodies, the "*green glands*" (Fig. 101, *40*) situated in the ventral part of the head anterior to the œsophagus. Each green gland consists of a glandular portion, green in color (*40*), a thin-walled dilatation, the bladder (*41*), and a duct opening to the exterior through a pore at the top of the papilla on the basal segment of the antenna (*42*).

Nervous System. — The morphology of the nervous system of the crayfish is in many respects similar to that of the earthworm. The *central nervous system* includes a dorsal ganglionic mass, the *brain* (Fig. 101, *25*), in the head, and two *circum-œsophageal connectives* (*26*) passing to the *ventral nerve cord* (*27*), which lies near the median ventral surface of the body.

Brain. — The brain (Fig. 101, *25*) is a compact mass larger than that of the earthworm, and supplies the eyes, antennules, and antennæ with nerves.

Ventral Nerve Cord. — The ganglia and connectives of the ventral nerve cord are more intimately fused than in the earthworm, and it is difficult to make out the double nature of the connectives, except between segments XI and XII, where the sternal artery passes through (Fig. 101, *30*). Each segment posterior to VII possesses a ganglionic mass, which sends nerves to the surrounding tissues. The large sub-œsophageal ganglion in segment VII consists of the ganglia of segments III–VII fused together. It sends nerves to the mandibles, maxillæ, and first and second maxillipeds.

The Visceral Nervous System consists of an anterior visceral nerve which arises from the ventral surface of the brain, is joined by a nerve from each circum-œsophageal connective, and, passing back, branches upon the dorsal wall of the pyloric part of the stomach, sending a *lateral nerve* on each side to unite with an *infero-lateral nerve* from the *stomatogastric ganglion*.

Sense Organs. — Eyes. — The eyes of the crayfish are situated

at the end of movable stalks which extend out, one from each side of the rostrum (Fig. 101, *28*). The external convex surface of the eye is covered by a modified portion of the transparent cuticle, called the *cornea*. This cornea is divided by a large number of fine lines into four-sided areas, termed *facets*. Each facet is but the external part of a long visual rod known as an *ommatidium* (Fig. 103).

Sections show the compound eye to be made up of similar ommatidia lying side by side, but separated from one another by a layer of dark pigment cells. The average number of ommatidia in a single eye is 2500 (180).

Two ommatidia are shown in Figure 103. Beginning at the outer surface, each ommatidium consists of the following parts: (*a*) a *corneal* facet (*1*), (*b*) two *corneagen* cells (*2*) which secrete the cornea, (*c*) a *crystalline cone* (*5*) formed by four cone cells, or *vitrellæ* (*3*), (*d*) two *retinular cells* surrounding the cone (not shown in Fig. 103), (*e*) seven

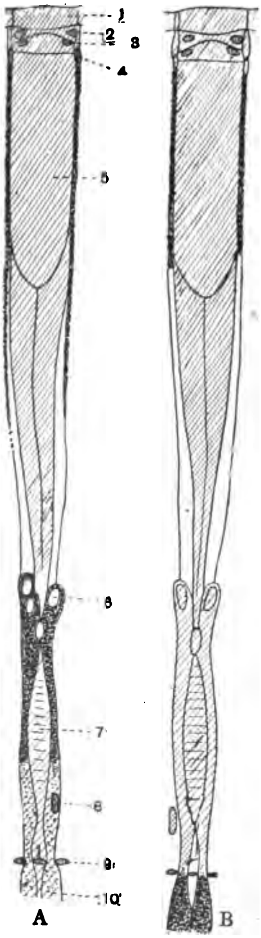


FIG. 103. Longitudinal sections of two ommatidia of the crayfish; A, pigment arranged as influenced by light; B, pigment arranged as influenced by darkness; *1*, cornea; *2*, nucleus of corneagen cells; *3*, nucleus of vitrella; *4*, nucleus of pigment cell; *5*, crystalline cone; *6*, tapetum cell; *7*, rhabdom; *8*, retinal cell; *9*, basement membrane; *10*, retinal nerve fiber. (From Sedgwick after Parker.)

retinular cells (*8*) which form a *rhabdom* (*7*) consisting of four *rhabdomeres*, and (*f*) a number of *pigment cells* (*4, 6*). Fibers from the *optic nerve* enter at the base of the ommatidium and communicate with the inner ends of the retinular cells (*10*).

VISION. — The *eyes* of the crayfish are supposed to produce an *erect mosaic* or "*apposition image*"; this is illustrated in Figure 104 where the ommatidia are represented by *a–e* and the fibers from the optic nerve by *a′–e′*. The rays of light from any point *a*, *b*, or *c*, will all encounter the dark pigment cells surrounding the ommatidia and be absorbed, except the ray which passes directly through the center of the cornea as *d* or *e*; this ray will penetrate to the retinulæ, and thence to the fibers from the optic nerve. "Thus the retinula of one ommatidium receives a single resultant impression from the light which reaches it. But the adjacent ommatidia being directed to a different, though adjoining, region of the outer world, may transmit a different impression, and the stimuli from all the ommatidia which make up a compound eye will correspond in greater or less degree to the whole of the visible outer world which subtends their several optic axes. The sum of the resulting images which we may thus suppose to be transmitted to the brain may be compared to a mosaic in which the effect is given by a large number of separate pieces, of one size and each of uniform colour" (183, p. 332). This method of image formation is especially well adapted for recording motion, since any change in the position of a large object affects the entire 2500 ommatidia.

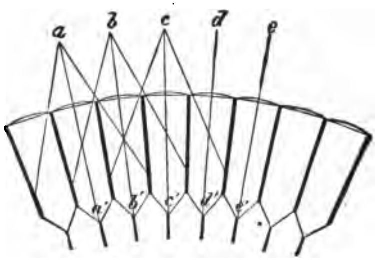


FIG. 104. Diagram to explain mosaic vision (see text.) (From Packard after Lubbock.)

When the pigment surrounds the ommatidia (Fig. 103, A), vision is as described above; but it has been found that in dim light the pigment migrates partly toward the outer and partly

toward the basal end of the ommatidia (Fig. 103, *B*). When this occurs the ommatidia no longer act separately, but a combined image is thrown on the retinular layer. "In this manner an erect '*superposition image*' is formed, the rays refracted by a large number of crystalline cones being superposed at the focus on the retina, and a stimulus far stronger in proportion to the intensity of the illumination than that of the apposition image, though probably much less distinct in detail, is given to the retinulæ" (183, p. 333).

STATOCYSTS. — The statocysts of *Cambarus* are chitinous-walled sacs situated one in the basal segment of each antennule. In the base of the statocyst is a ridge, called the *sensory cushion*, and three sets of *hairs*, over two hundred in all, each innervated by a single nerve fiber. Among these hairs are a number of large grains of sand, the *statoliths*, which are placed there by the crayfish. Beneath the sensory cushion are *glands* which secrete a substance for the attachment of the statoliths to the hairs (181).

The statocyst for many years was considered an auditory organ, and it may possibly function as such, though recent investigations have proven that it is primarily an organ of *equilibration*. The contact of the statoliths with the statocyst hairs determines the orientation of the body while swimming, since any change in the position of the animal causes a change in the position of the statoliths under the influence of gravity. When the crayfish changes its exoskeleton in the process of molting, the statocyst is also shed. Individuals that have just molted, or have had their statocysts removed, lose much of their powers of orientation. Perhaps the most convincing proof of the function of equilibration is that furnished by the experiments of Kreidl (172). This investigator placed shrimps, which had just molted and were therefore without statoliths, in filtered water. When supplied with iron filings, the animals filled their statocysts with them. A strong electro-magnet was then held near the statocyst, and the shrimp took up a position corresponding to the resultant of the two pulls, that of gravity and of the magnet.

Muscular System. — The principal muscles in the body of the crayfish are situated in the abdomen, and are used to bend that part of the animal forward upon the ventral surface of the thorax, thus producing backward locomotion in swimming. Other muscles extend the abdomen in preparation for another stroke. Figure 100 shows a cross section of an abdominal segment. The powerful flexor muscles (*FM*) occupy almost the entire abdominal space. In the dorsal region are the less powerful extensor muscles (*EM*). Other muscles of considerable size are situated within the tubular appendages, especially the chelipeds. Figure 105 shows how the muscles of a walking leg are arranged. A comparison of the skeleton and muscles of the crayfish with those of man is interesting. The skeleton of the crayfish is external and tubular, except in the ventral part of the thorax (Fig. 101, *39*). The muscles are internal, and attached to the inner surface of the skeleton. In man, on the other hand, the skeleton is internal and the muscles external.

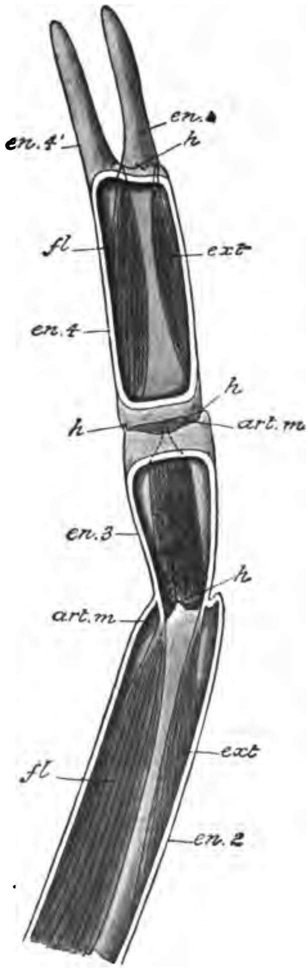


FIG. 105. Part of the leg of a crayfish showing muscles. (From Parker and Haswell.)

Reproductive System. — Crayfishes are normally *diœcious*, there being only a few cases on record where both male and

female reproductive organs were found in a single specimen.

MALE REPRODUCTIVE ORGANS.—The male organs (Fig. 106) consist of a *testis* and two *vasa deferentia* (*3*) which open through the coxopodites of the fifth pair of walking legs (*4*, *5*). The testis lies just beneath the pericardial sinus. It is a soft white body possessing two anterior lobes (Fig. 106, *1*) and a median posterior extension (*2*). The vasa deferentia are long coiled tubes.

FIG. 106. Male reproductive organs of the crayfish. *1*, right anterior lobe of testis; *2*, posterior lobe of testis; *3*, vas deferens; *4*, external opening of vas deferens; *6*, base of fifth walking leg. (From Shipley and MacBride.)

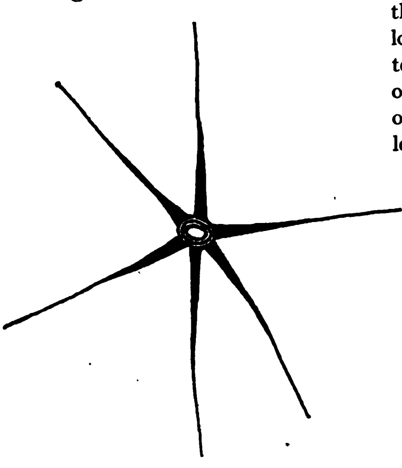


FIG. 107. A spermatozoon of the crayfish. (From Andrews, in *Anat. Anz.*)

SPERMATOGENESIS. — The primitive germ cells within the testis pass through two maturation divisions, and then metamorphose into spermatozoa. These are flattened spheroidal bodies when inclosed within the testis or vas deferens, but if examined in water or some other liquid they are seen to uncoil, finally becoming star-shaped (Fig. 107).

The spermatozoa remain in the testis and vasa deferentia until copulation takes place. As many as two million spermatozoa are contained in the vasa deferentia of a single specimen (158).

Female Reproductive Organs. — The *ovary* resembles the testis in form, and is similarly located in the body (Fig. 108). A short *oviduct* (*1*) leads from near the center of each side of the ovary to the external aperture in the coxopodite of the third walking leg (*4*, *5*).

Oogenesis. — The primitive germ cells in the walls of the ovary grow in size, become surrounded by a layer of small cells, the follicle, which eventually break down, allowing the eggs to escape into the central cavity of the ovary. At the time of laying the ova pass out through the oviduct.

Breeding Habits. — The details of copulation, egg-laying, and the larval stages of *Cambarus* have only recently been made out, and even now our account must be derived from observations of several different species, since the entire life history of a single species has never been recorded. The development of the eggs of *Cambarus* from the time of deposition to the time of hatching has likewise never been investigated.

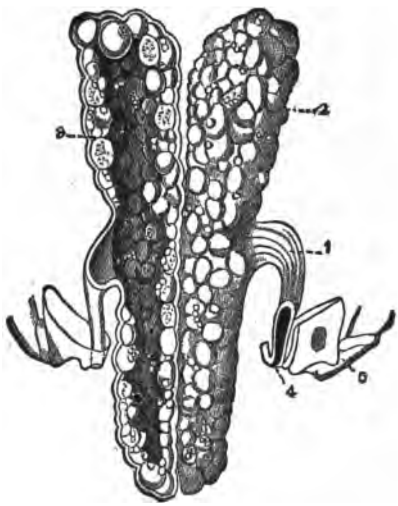


Fig. 108. Female reproductive organs of the crayfish. *1*, right oviduct; *2*, right lobe of ovary; *3*, left lobe opened to show central cavity; *4*, external opening of oviduct; *5*, base of third walking leg. (From Shipley and MacBride.)

The principal events in the reproduction of crayfishes may be enumerated as follows: —

(1) Copulation, during which the spermatozoa are transferred from the vasa deferentia of the male to the seminal receptacle of the female; (2) egg-laying; (3) the embryonic development of the eggs; (4) hatching; (5) the growth of the young crayfishes.

COPULATION. — Copulation in crayfishes, in most cases, takes place in September, October, or November of the first year of

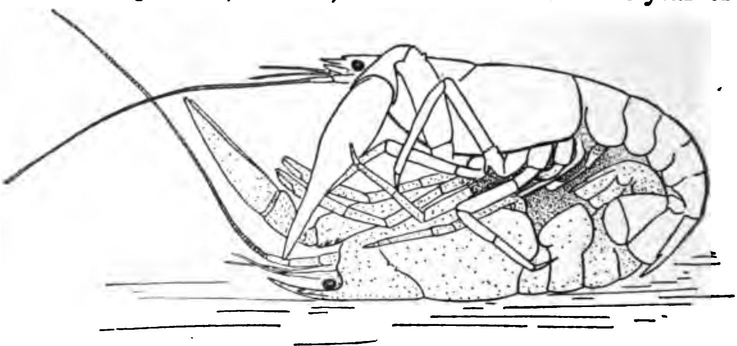


FIG. 109. Male crayfish transferring spermatozoa to the seminal receptacle of the female. (From Andrews in *Am. Nat.*)

their lives, that is, when they are about four months old. A second copulating season is passed through at the end of the second summer, when the animals are about seventeen months old, and a third copulating season occurs at the end of the third summer (179). At these times a male approaches a female, grasps her by her cephalic appendages, and, after a struggle, turns her over on her back. He then stands over her in the position shown in Figure 109, and transfers spermatozoa to the seminal receptacle. During this process, the spermatozoa flow out of the openings of the vasa deferentia, pass along the grooves on the first abdominal appendages of the male (Fig. 101, *14*), and enter the seminal receptacle (159). Here they are stored during the winter. The *seminal receptacle* is a cavity in a fold of cuticle lying between the

sterna of the segments bearing the fourth and fifth pairs of walking legs.

EGG-LAYING (159, 160). — The eggs are laid at night during the month of April. First the ventral side of the abdomen is thoroughly cleaned of all dirt by the hooks and comb-like bristles near the end of the fifth pair of walking legs. A clear slime or *glair* is secreted by *cement glands* situated chiefly on the basal parts of the uropods, and on the endopodites of the other abdominal appendages. This milky glair gradually covers the swimmerets. The female then lies on her back, and an apron-like film of glair is constructed between the ends of the uropods and telson, and the bases of the second pair of walking legs (Fig. 110).

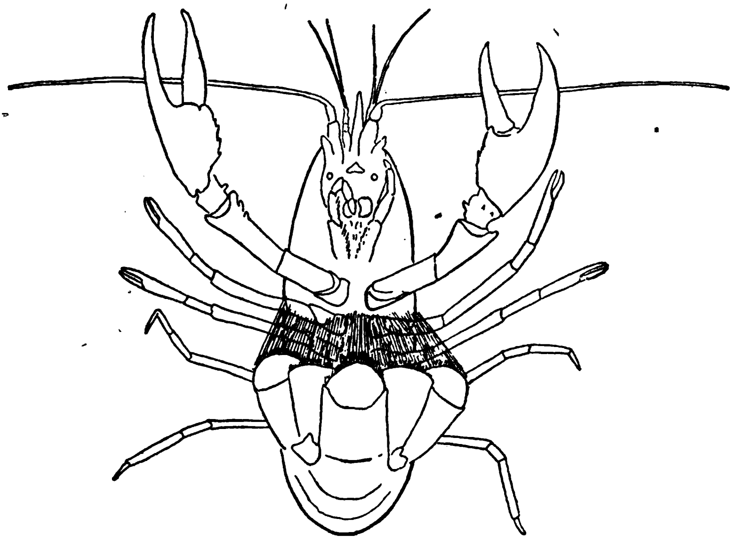


FIG. 110. Female crayfish lying on back laying eggs. (From Andrews in *Am. Nat.*)

The eggs emerge from the openings of the oviducts in the bases of the third pair of walking legs, flow posteriorly, and become attached to the hairs on the swimmerets by strings of a substance

no doubt secreted by the cement glands. This is brought about by the turning of the animal first on one side and then on the other a number of times. From one hundred to over six hundred greenish eggs are laid by a single female, depending upon the size and age of the animal. After the eggs are laid the crayfish rights herself, the apron of glair breaks down, and the abdomen is extended (Fig. 111).

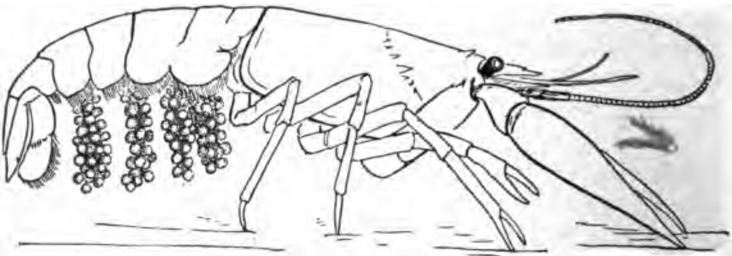


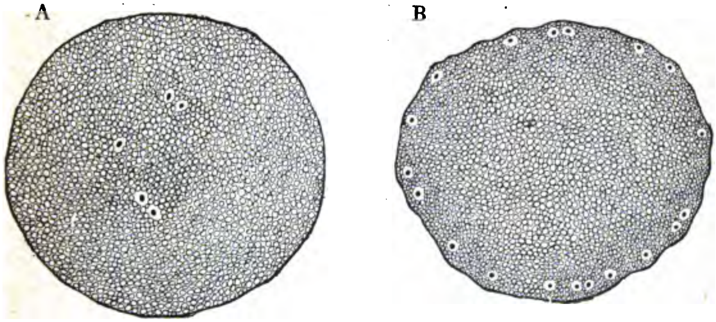
FIG. 111. Female aerating eggs by raising and straightening abdomen and waving swimmerets back and forth. (From Andrews in *Am. Nat.*)

FERTILIZATION. — The method of fertilization has never been discovered. It is supposed that as the eggs are laid they pass over the opening of the seminal receptacle, and are then penetrated by the spermatozoa which were placed there by the male the preceding autumn (160).

Embryology. — While the eggs are developing they are protected by the abdomen of the female, and are *aerated* and kept free from dirt by the waving of the swimmerets back and forth (Fig. 111). The embryology of *Cambarus* has never been investigated, but it probably resembles closely the development of the common European crayfish, *Astacus fluviatilis*.

The fertilized egg of *Astacus* consists of a large number of *yolk spheres* embedded in *cytoplasm*, and contains a *nucleus* composed of the egg nucleus and the spermatozoon combined. This nucleus proceeds to form two daughter nuclei. The egg does not become divided into two parts by cell walls, but the daughter nuclei separate from one another and divide again

(Fig. 112, A). This division continues until there are a large number of nuclei scattered about among the yolk spheres. Finally all of the nuclei migrate toward the periphery of the egg and come to lie just beneath the surface (Fig. 112, B). Cell walls then appear, dividing the egg into as many *yolk pyramids* as there are nuclei (Fig. 112, C). The outer ends of these yolk pyramids containing the nuclei are now cut off by cross walls, the result being a single layer of cells, the *blastoderm*, surrounding the entire egg. The side walls of the inner portion of the pyramids fuse, partially restoring the original condition.



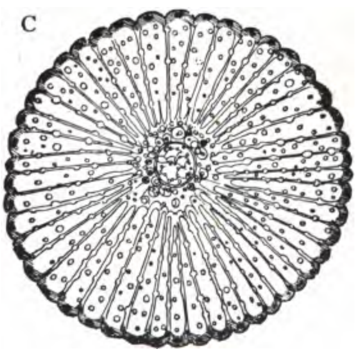


FIG. 112. Three stages in the development of the egg of the crayfish. A, a few cleavage nuclei in the egg; B, nuclei arranged near the surface; C, egg divided into yolk pyramids. (From Korschelt and Heider. A and B, after Morin; C, after Reichenbach.)

The embryology of the crayfish is so complex that a detailed account will not be attempted here. It will suffice to make a superficial examination of the developing embryo with the aid of Figures 112–115. A thickening of the blastoderm on one side of the egg is known

as the *primitive streak.* Five other thickenings also arise in this region, a pair of *optic lobes* (Fig. 113, *K*) a pair of *thoraco-abdominal plates* (*TA.*), and a median *entodermal plate* (*ES.*). The side on which these thickenings occur will become the ventral surface of the adult.

A later stage (Fig. 114) shows a median outgrowth just back of the optic lobes which will become the upper lip, or *labrum* (*l*), and pairs of rudimentary *antennules* (a_1), *antennæ* (a_2) and *mandibles* (*m*). Between the antennæ is a depression, which will become the *mouth.* An opening in the thoraco-abdominal plate (*TA.*) represents the future *anus* (*A*). In a more advanced embryo (Fig. 115) the structures already mentioned are seen in a later stage of development. The thoraco-abdominal rudiment has become divided into a number of segments, from each of which a pair of appendages arise and develop into those of the adult crayfish (171). The length of time required for the various stages in development was found by Andrews to be as follows: "Cleavage took up the first week, the beginning of an embryo the second week, to progress as far as the Nauplius the third week and more, to enlarge the embryo over one half of the egg a fourth week and more, and to perfect the embryo for hatching a fifth and sixth week or more. The whole egg development required from five to eight weeks in different sets of eggs under different temperature" (159, pp. 189–190).

HATCHING (159, 163). — In hatching, the egg capsule splits and the larva emerges head foremost. The helpless young crayfish would drop away from the mother at once but for a thread extending from its telson to the inner surface of the egg capsule (Fig. 116).

Soon the larva possesses strength enough to grasp the egg string with its claws (Fig. 116). The telson thread then breaks. After about forty-eight hours the larva passes into a *second stage.* This is inaugurated by the shedding of the first larval cuticular covering, a process known as *molting* or *ecdysis.* This casting off of the covering of the body is not peculiar to the young, but occurs

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in adult crayfishes as well as in young and adults of many other animals. In the larval crayfish the cuticle of the first stage becomes loosened and drops off. In the meantime the hypodermal cells have secreted a new covering. Ecdysis is necessary before growth can proceed, since the chitin of which the exoskeleton is composed does not allow expansion. In adults it is also a means of getting rid of an old worn-out coat and acquiring a new one.

In the *second larval stage* the young crayfish is again supported immediately after casting off its covering by a thread extending from the new to the old telson. When the larva becomes strong

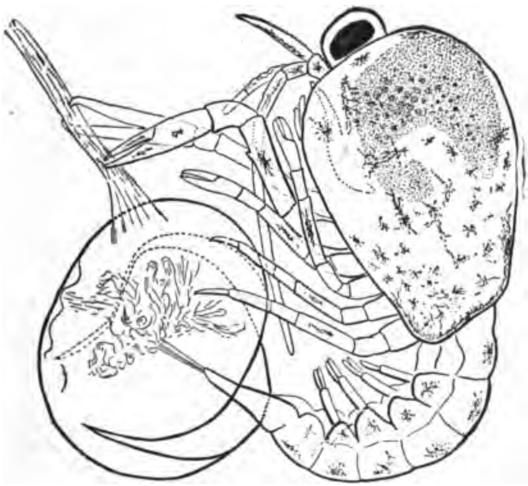


FIG. 116. Larva of crayfish 24 hours after hatching; claws fastened to stalk of eggshell and abdomen fastened to inside of shell. (From Andrews in *Am. Nat.*)

enough, it grasps the old larval skin or swimmerets, and the telson thread drops off. The duration of the second larval stage is about six days.

No telson thread is present after the molt which ushers in the *third larval stage*, but the young is able at once to cling to the old cuticle. In about a week the third larvæ become entirely inde-

TABLE IX

THE DURATION OF THE LARVAL STAGES, AND THE SIZE AND HABITS OF YOUNG CRAYFISHES DURING THE FIRST SUMMER

Stage	Duration	Size	Habit
1st	2 days	4 mm.	Attached to mother.
2d	6 days	5 mm.	Attached to mother.
3d	18 days	8 mm.	Associated with mother for one week, then free.
4th	17 days	12 mm.	Free.
5th	5 days	17 mm.	Free.
6th	11 days	21 mm.	Free.
7th	?	29 mm.	Free.
End of summer	4 months	41 mm.	Free.

pendent of the mother, although they at first always return to her when separated. From this time on the larvæ shift for themselves,

TABLE X

THE AVERAGE RATE OF GROWTH OF A CRAYFISH (*Cambarus affinis*)

Age	Time Interval	Size
Just hatched		4 mm.
End of 1st summer	4 months	41 mm.
End of 2d summer	16 months	74 mm.
End of 3d summer	28 months	90 mm.
End of 4th summer	40 months	98 mm.

growing rapidly, and molting at least four more times during the first summer. The first winter no growth nor molts occur. There are four or five molts the second summer, three or four in the third summer, and perhaps one or two in the fourth summer.

The life of a single individual extends over a period of about three or more years. Table IX presents the main facts of larval development during the first summer (159). Table X gives the age and size of a single specimen during its entire life.

Regeneration. — The crayfish and many other Crustaceans have the power of regenerating lost parts, but to a much more limited extent than such animals as *Hydra* and the earthworm. Experiments have been performed upon almost every one of the appendages as well as the eye. The second and third maxillipeds, the walking legs, the swimmerets, and the eye have all been injured or extirpated at various times and subsequently renewed the lost parts. Many species of crayfish of various ages have been used for these experiments. The growth of regenerated tissue is more frequent and rapid in young specimens than in adults (184).

The new structure is not always like that of the one removed. For example, when the annulus containing the sperm receptacle of an adult is extirpated, another is regenerated, but, although this is as large as that of the adult, it is comparable in complexity to that of an early larval stage (161). A more remarkable phenomenon is the regeneration of an apparently functional (tactile) antenna-like organ in place of a degenerate eye which was removed from the blind crayfish, *Cambarus pellucidus testii*. In this case a non-functional organ was replaced by a functional one of a different character (190). The regeneration of a new part which differs

FIG. 117. Diagram showing antenna-like organ regenerated in place of an eye of Palæmon. (From Morgan after Herbst.)

from the part removed is termed *heteromorphosis*. Figure 117 shows an antenna which regenerated in place of an eye in a marine crustacean, *Palæmon*. Instances of heteromorphosis have also been recorded in experiments on other animals (176).

Autotomy. — Perhaps the most interesting morphological structure connected with the regenerative process in *Cambarus* is the definite breaking point near the bases of the walking legs. If the chelæ are injured, they are broken off by the crayfish at the breaking point. The other walking legs, if injured, may be thrown off at the free joint between the second and third segments. A new leg, as large as the one lost, develops from the end of the stump remaining. This breaking off of the legs at a definite point is known as autotomy, a phenomenon that also occurs in a number of other animals. The leg is separated along the breaking point by several successive muscular contractions. It has been shown "that autotomy is not due to a weakness at the breaking point, but to a reflex action, and that it may be brought about by a stimulation of the thoracic ganglion as well as by a stimulation of the nerve of the leg itself" (182, p. 310). Immediately after the leg has been thrown off, a membrane of ectoderm cells covers the canal through which the nerve and blood passed; five days later regeneration begins by an outward growth of the ectoderm cells which lined the exoskeleton. An interesting point in this new growth is that the muscles of the regenerated part are probably produced by ectoderm cells, whereas in the embryonic development of the crayfish the muscles are supposed to arise from the entoderm (178).

The power of autotomy is of advantage to the crayfish, since the wound closes more quickly if the leg is lost at the breaking point. No one has yet offered an adequate theory to account for autotomy. It is probably "a process that the animal has acquired in connection with the condition under which it lives, or in other words, an adaptive response of the organism to its condition of life" (176, p. 158).

As in the earthworm, the *rate of regeneration* depends upon the

amount of tissue removed. If one chela is amputated, a new chela regenerates less rapidly than if both chelæ and some of the other walking legs are removed (189).

Behavior. — When at rest, the crayfish usually faces the entrance to its place of concealment, and extends its antennæ. It is thus in a position to learn the nature of any approaching object without being detected. Activity at this time is reduced to the movements of a few of the appendages and the gills; the scaphognathites of the second maxillæ move back and forth baling water out of the forward end of the gill chambers; the swimmerets are in constant motion creating a current of water; the maxillipeds are likewise kept moving; and the antennæ and eye stalks bend from place to place.

Crayfishes are more active at nightfall and at daybreak than during the remainder of the day. At these times they venture out of their hiding places in search of food, their movements being apparently all utilitarian and not for spontaneous play or exercise (167).

Locomotion. — Locomotion is effected in two ways, walking and swimming. Crayfishes are able to walk in any direction, forward usually, but also sidewise, obliquely, or backward. In walking, the fourth pair of legs are most effective and bear nearly all of the weight of the animal; the fifth pair serve as props, and to push the body forward; the second and third pairs are less efficient for walking, since they are modified to serve as prehensile organs, and as toilet implements (168). Swimming is not resorted to under ordinary conditions, but only when the animal is frightened or shocked. In such a case the crayfish extends the abdomen, spreads out the uropods and telson, and, by sudden contractions of the bundles of flexor abdominal muscles, bends the abdomen and darts backwards. The swimming reaction apparently is not voluntary, but is almost entirely reflex (168).

Equilibration. — The crayfish either at rest or in motion is in a state of unstable equilibrium, and must maintain its body in the normal position by its own efforts. The force of gravity tends

to turn the body over. From a large number of experiments it has been proven that the statocysts are the organs of equilibration. The structure of these organs is described on page 208. The contact of the statoliths with the statocyst hairs furnishes the stimulus which causes the animal to maintain an upright position.

When placed on its back, the crayfish has some difficulty in righting itself. Two methods of regaining its normal position are employed. The usual method is that of raising itself on one side and allowing the body to tip over by the force of gravity. The second method is that of contracting the flexor abdominal muscles which causes a quick backward flop, bringing the body right side up (168). In general, the animals " right themselves, when placed on their backs, by the easiest method; and this is found to depend usually upon the relative weight of the two sides of the body. When placed upon a surface which is not level, they take advantage, after a few experiences, of the inclination by turning toward the lower side " (188, p. 577).

SENSES AND THEIR LOCATION. — The sense of *touch* in crayfishes is perhaps the most valuable, since it aids them in finding food, avoiding obstacles, and in many other ways. It is located in specialized hairs on various parts of the body (164). *Vision* in crayfishes is probably of minor importance, since the compound eyes are almost useless in recognizing form, and are of real value only in detecting moving objects. No reactions to *sound* have ever been observed in crayfishes, and apparently they do not hear. " The reactions formerly attributed to audition are probably due to tactile reflexes " (181, p. 244). In aquatic animals it is so difficult to distinguish between reactions of *taste* and *smell* that these senses are both included in the term *chemical sense.* The end organs of this sense are distributed all over the body.

REACTIONS TO STIMULI. — THIGMOTROPISM. — The crayfish " is sensitive to touch over the whole surface of the body, but especially on the chelæ and chelipedes, the mouth parts, the ventral surface of the abdomen, and the edge of the telson " (164, p. 644).

The antennæ are usually considered the special organs of touch, but experiments seem to prove that they are not so sensitive as other parts of the body. The tactile hairs are plumed, and supplied by a single nerve. *Positive thigmotropism* is exhibited by crayfishes to a marked degree, the animals seeking to place their bodies in contact with a solid object, if possible. The normal position of the crayfish when at rest under a stone is such as to bring its sides or dorsal surface in contact with the walls of its hiding place. Thigmotropism, no doubt, is of distinct advantage, since it forces the animal into a place of safety.

PHOTOTROPISM. — Light of various intensities in the majority of cases causes the crayfish to retreat, *i.e.* to show *negative phototropism.* Individuals prefer colored lights to white, having a special liking for red. Negative reactions to light play an important rôle in the animal's life, since they influence it to seek a dark place where it is concealed from its enemies.

CHEMOTROPISM. — The reactions of the crayfish to food are due in part to a chemical sense. Smooth hairs, with nerve bundles within them, are probably chemical, and, since "The animals react to chemical stimulation on any part of the body . . . we must assume that there are chemical sense organs all over the body" (165, p. 325). The anterior appendages, however, are the most sensitive, especially the outer ramus of the antennule. *Positive reactions* result from the application of food substances. For example, if meat juice is placed in the water near an animal, the antennæ move slightly and the mouth parts perform vigorous chewing movements. The meat causes "general restlessness and vague movements toward the source of the stimulation, but the animals seem to depend chiefly on touch for the accurate localization of food" (165, p. 326). Acids, salts, sugar, and other chemicals produce a sort of *negative reaction* indicated by scratching the carapace, rubbing the chelæ, or pulling at the part stimulated.

HABIT FORMATION. — It has been shown by certain simple experiments that crayfishes are able to learn habits and to modify

them. They learn by experience, and modify their behavior slowly or quickly, depending upon their familiarity with the situation. The following experiments prove the above statements. Crayfishes, when placed in compartment *T* of a labyrinth like that shown in Figure 118, will, on attempting to escape, pass on one side or the other of the partition *P*. A transparent glass screen *G* prevents their exit from the right side of the partition; the other side, however, being left open, allows a free passage. It was found by Yerkes and Huggins (188) that after sixty trials, crayfishes that at the beginning chose the closed passage 50 per cent of the time, learned to avoid that side, and in 90 per cent of the trials chose the open exit. When the glass plate was then removed from the right of the partition and placed on the other side, the crayfishes were confused at first, but learned the new habit of escaping at the right, open side more quickly than before. The "chief factors in the formation of such habits are the chemical sense (probably both smell and taste), touch, sight, and the muscular sensations resulting from the direction of turning. The animals are able to learn a path when the possibility of following a scent is excluded" (188, p. 577). Professor S. J. Holmes writes that he has trained crayfishes to come to him for food.

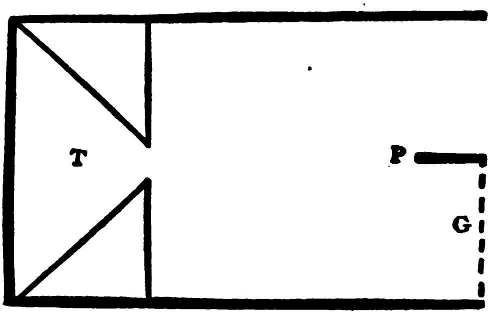


FIG. 118. Labyrinth used in experiments on the crayfish. *T*, compartment from which animal was started; *P*, partition at exit; *G*, glass plate closing one exit. (From Washburn after Yerkes and Huggins.)

2. Arthropods in General

All the segmented animals bearing jointed appendages belonging to the Phylum Arthropoda may be grouped in five classes:—

Class I. Crustacea (Crayfish, Crabs, Barnacles, Water-fleas, etc.).

Class II. Onychophora (Peripatus).

Class III. Myriapoda (Centipedes and Millipedes).

Class IV. Insecta (Insects).

Class V. Arachnida (Spiders, Mites, Scorpions, King crabs, etc.).

These five classes are often divided for convenience into two large groups, the Branchiata containing Class I, and the Tracheata, Classes II–V. Members of the former division are mainly aquatic and breathe by means of gills. The Tracheata are in most cases terrestrial, and obtain oxygen from air taken into a complex system of tubules, called tracheæ, which ramify to all parts of the body.

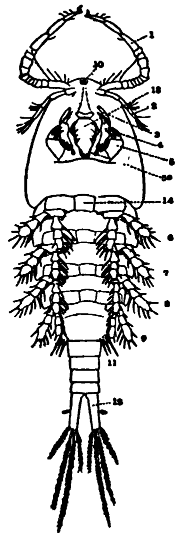


FIG. 119. Ventral view of male *Cyclops*. *1*, antennule; *2*, antenna; *3*, mandible; *4*, 1st maxilla; *5*, two halves of 2d maxilla; *6–9*, 1st–4th thoracic limbs; *10*, eye; *11*, bristles near male genital opening; *12*, caudal fork; *13*, mouth; *14*, copula connecting pairs of limbs. (From Shipley and MacBride.)

Arthropods are supposed to be closely related to Annelids. The members of both phyla are segmented, bilaterally symmetrical, and triploblastic, with a dorsal brain in the head and a ventral nerve cord, a dorsal heart, and an external chitinous covering. The following differences may be pointed out: Annelids possess a large number of similar segments; Arthropods, in most cases, a limited number of much modified segments: the former have segmentally arranged nephridia; the excretory organs of the latter,

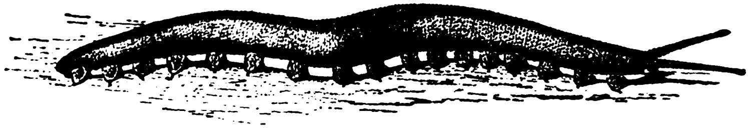


FIG. 120. *Peripatus capensis.* (From Shipley and MacBride after Sedgwick.)

with the exception of *Peripatus*, are not segmentally arranged; Annelids have a well developed cœlom; in arthropods the cœlom is restricted to the cavities of the excretory and reproductive organs.

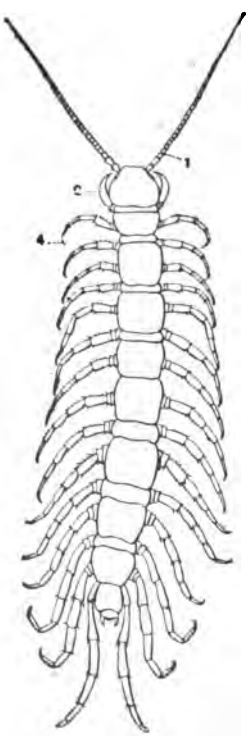


FIG. 121. Dorsal view of a centipede. *1*, antenna; *2*, poison claw. (From Shipley and MacBride.)

The Crustacea are divided into two subclasses, the Entomostraca and the Malacostraca. The Entomostraca includes most of the small simple species (Fig. 119). These have a variable number of segments; no gastric mill in the stomach; and in many species hatch as a larval form called a *Nauplius* (Fig. 126, A). The Malacostraca are usually large. They have a definite number of segments — five in the head, eight in the thorax, and six in the abdomen; the stomach contains a gastric mill; and the Nauplius stage is usually passed through within the egg before hatching. The crayfish belongs in this subclass.

Class Onychophora contains only a few annelid-like animals, the best known being *Peripatus capensis* (Fig. 120). Segmentally arranged nephridia, stump-like legs, simple eyes, and tracheæ are some of the organs possessed by members of this class.

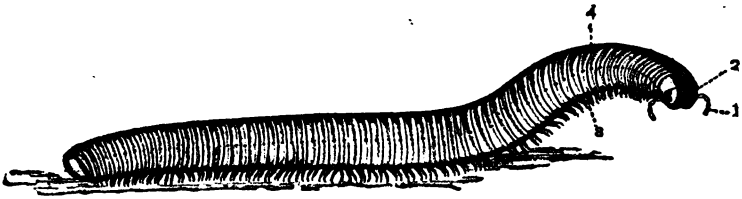


FIG. 122. A millipede. (From Shipley and MacBride after Koch.)

The myriopods are also annelid-like in appearance. The two principal orders are the Chilopoda and Diplopoda. The Chilopoda or centipedes (Fig. 121) are flattened dorso-ventrally, have one pair of legs attached to every segment back of the head, and possess a pair of poison claws attached to the first segment. The Diplopoda or Millipedes (Fig. 122) are cylindrical, have two pairs of legs attached to every segment back of the fourth, and lack poison claws.

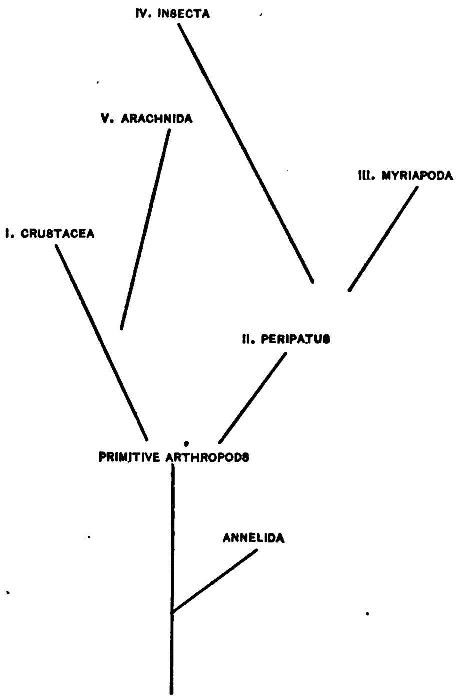


FIG. 123. Diagram to show the affinities of arthropods.

The insects constitute about four fifths of all the species of animals. The number of individuals is even more remarkable. The body of an insect is divided into head, thorax, and abdomen. The thorax

bears three pairs of legs, and, with a few exceptions, one or two pairs of wings. The abdomen has several or no appendages. The honeybee described in Chapter XII has been selected as a type of this class.

The Class Arachnida includes animals which have the head and thorax fused into a cephalo-thorax. They possess four pairs of legs, an abdomen usually without appendages, and a heart in the dorsal part of the abdomen. Such diverse animals as the spider, scorpion, mite, and King crab are placed together in this class. The probable affinities of the various classes of arthropods are shown in Figure 123.

The Biogenetic Law. — In concluding this chapter we wish to refer to a law which has commanded the attention of zoologists for almost a century; namely, the law of biogenesis, also known as the *recapitulation theory.* Organic evolution, that is, the evolution of one organism from another, is accepted as an established fact by practially all zoologists at the present time. This fact of organic evolution is expressed in the diagram of the principal phyla of the animal kingdom on page 7, where the various groups appear to be derived from a central stem which represents a series of ancestral forms. From an examination of the phyla represented in our diagram we gain the fact that the members of each group are more complex than those of the group just beneath them on the page. Evolutionists do not claim that the more complex forms have evolved directly from the simpler animals, but that their ancestors were related. Beginning with the simplest animals we find that a single cell performs all the necessary processes of life, *e.g. Ameba.* Within the lowest phylum, the Protozoa, there are animals consisting of a number of cells more or less intimately bound together into a hollow spherical colony, *e.g. Volvox.* Passing to the next higher group of organisms we are introduced to animals that possess two layers of cells, surrounding a single cavity, *e.g. Hydra.* All animals above the Cœlenterates have three layers of cells forming their body walls, *i.e.* are triplo-

blastic. Four stages in the evolution of animals are represented in the groups just mentioned — (1) the single cell, (2) a ball of cells, (3) a two-layered sac, and (4) a three-layered organism.

Early in the past century it was noticed that these stages correspond to the early stages in the embryology of the Metazoa; in other words, that the development of the individual recapitulates the stages in the evolution of the race, or ontogeny recapitulates phylogeny. These stages contrasted appear as follows: —

Phylogenetic Stage	*Ontogenetic Stage*
(1) single-celled animal	egg cell.
(2) ball of cells	blastula.
(3) two-layered sac	gastrula.
(4) triploblastic animal	three-layered embryo.

Later other zoologists became interested in the recapitulation theory, and enlarged upon it. Of these Fritz Müller and Ernst Haeckel are especially worthy of mention. The latter expressed the facts as he saw them in his "fundamental law of biogenesis." The ancestor of the many-celled animals was conceived by him as a two-layered sac something like a gastrula, which he called a *Gastræa*. The Cœlenterates were considered to be gastræa slightly modified.

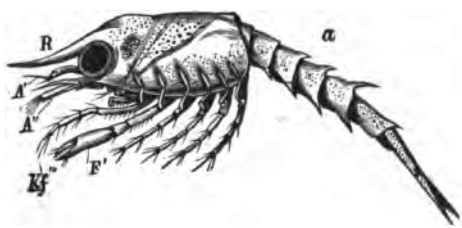


FIG. 124. Larva of lobster in *Mysis* stage. (From Sedgwick after Sars.)

Fritz Müller derived strong arguments in favor of biogenesis from a study of certain Crustacea belonging to the Malacostraca. Many members of this group do not emerge from the egg so

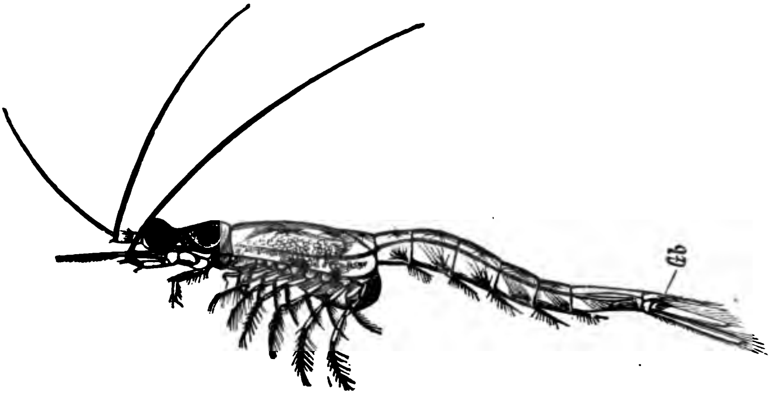
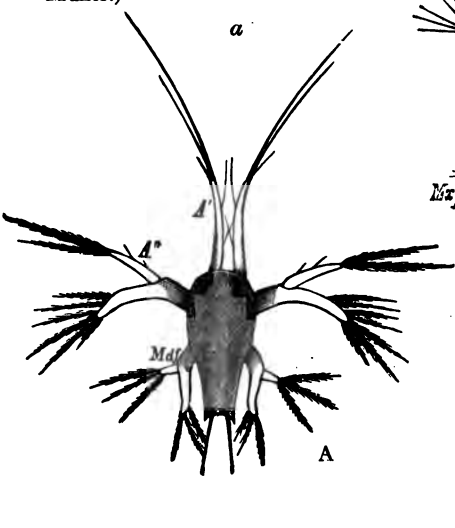
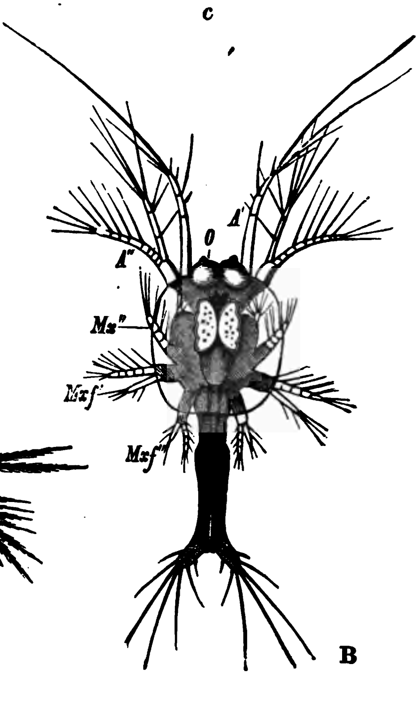


FIG. 125. *Mysis oculata*. (From Sedgwick after Sars.)

nearly like the adult as does the crayfish. The lobster, for ex-

FIG. 126. Two stages in the development of the shrimp, *Penæus*. A, *Nauplius* stage; B, *Protozoœa* stage. (From Sedgwick after Fritz Müller.)





ample, upon hatching (Fig. 124) resembles a less specialized prawn-like crustacean, called *Mysis* (Fig. 125), and is said to be in the *Mysis* stage. The shrimp, *Penæus*, passes through a number of interesting stages before the adult condition is

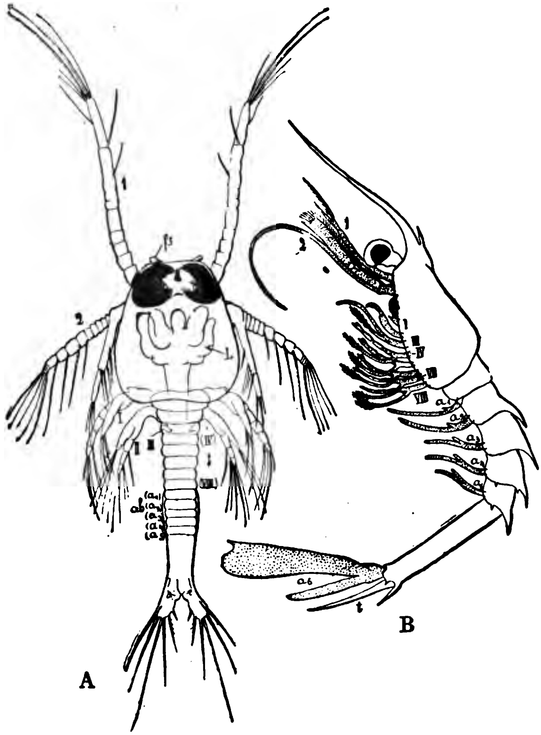


FIG. 127. Two later stages in the development of *Penæus*. A, *Zoœa* stage; B, *Mysis* stage. (From Korschelt and Heider after Claus.)

attained. It hatches as a larva, termed a *Nauplius* (Fig. 126, A), possessing a frontal eye and three pairs of appendages (*A′*, *A″*, *Mdf.*); this Nauplius molts and grows into a *Protozoœa* stage (Fig. 126, B) which bears three more pairs of appendages and the rudiments of segments III–VIII. The Protozoæa stage

grows into the *Zoœa* stage (Fig. 127, A). The cephalothorax and abdomen are distinct at this time; eight pairs of appendages are present (I–VIII) and six more are developing (a_1–a_6). The Zoæa grows and molts and becomes a *Mysis* (Fig. 127, B) with eight pairs of appendages (I–VIII) on the cephalothorax. Finally the *Mysis* passes into the adult shrimp, which possesses the characteristic number of appendages (I–XIX) each modified to perform its particular function. The *Nauplius* of *Penæus* resembles the larvæ of many simple crustaceans; the *Zoœa* is somewhat similar to the condition of an adult *Cyclops* (Fig. 119); the *Mysis* is like the adult *Mysis* (Fig. 125); and finally the adult *Penæus* is more specialized than any of its larval stages, and belongs among the higher Crustacea. The above facts have convinced some zoologists that *Penæus* recapitulates in its larval development the progress of the race; that the lobster has lost many of these stages, retaining only the *Mysis;* and that the crayfish hatches in practically the adult condition. The *Nauplius* stage of the latter is supposed to be represented by a certain embryonic phase (Fig. 114).

The law of biogenesis should not be taken too seriously, since it has been criticized severely by many prominent zoologists, but it has furnished an hypothesis, which has concentrated the attention of scientists upon fundamental embryological processes, and has therefore had a great influence upon zoological progress (175, 177, 187).

CHAPTER XII

THE HONEYBEE AND BEES IN GENERAL

1. The Honeybee

(*Apis mellifica* Linn.)

The honeybee has been selected as a type of the Class Insecta, of the Phylum Arthropoda, because of its wonderful adaptations to its environment; its complex social life; its economic value to man; and the ease with which it may be obtained for dissection, or studied alive in the laboratory. Honeybees have been made the objects of investigation by naturalists for over two thousand years, and the habits of no other insect are better known. They live in colonies in which there are three kinds of individuals — workers, drones, and a queen. An average colony contains in the summer about sixty thousand worker bees, a few hundred drones, and a single queen. The greatest number will be found in a hive during the honey-gathering season. In the winter the number diminishes by several thousands. No drones are members of the colony at this time. The appearance and functions of the different kinds of individuals found in one hive are as follows.

The Queen. — The queen (Fig. 128) is the most important member of the hive, since normally upon her and her alone falls the duty of reproduction. She lays all of the eggs, and is the mother of every worker and drone in the colony. She lives for three years or more, receiving during this time the support of her many offspring. The queen may be distinguished from the worker by the greater length of her abdomen and the absence of a pollen basket on the tibia of her hind legs.

The Drone. — The drone (Fig. 128) is the male bee; he lives in idleness upon the food gathered by the workers. His function, however, is an important one; namely, to mate with the queen. How this is accomplished will be described later. The body of the drone is heavy and broad, and the hind legs possess no pollen basket. His eyes are considerably larger than those of either the queen or worker.

The Worker. — The worker (Fig. 128) is a sexually undeveloped female. Under normal conditions it lays no eggs, but is kept

Worker Queen Drone

FIG. 128. Honeybee, *Apis mellifica.* (From Shipley and MacBride.)

busy gathering honey, pollen, and propolis, or "bee-glue," carrying water, secreting wax, building comb, preparing food, nursing the young, and cleaning and defending the hive. The workers are smaller than either queen or drone; they are the bees usually seen hovering about flowers. The anatomical description that follows concerns the worker unless otherwise stated.

Anatomy and Physiology. — EXOSKELETON. — The body of the bee is completely covered with a skin or cuticle, consisting of a very thin layer of chitin which is secreted by the hypodermal cells lying just beneath it. This chitin protects the insect from injury and gives the body strength. During the young stages the exoskeleton of inelastic chitin is cast off at intervals, allowing the body to expand.

REGIONS OF THE BODY. — Three distinct regions may be recognized in the body of the bee — the head, thorax, and abdomen. Each division consists of a definite number of segments more or less intimately fused together.

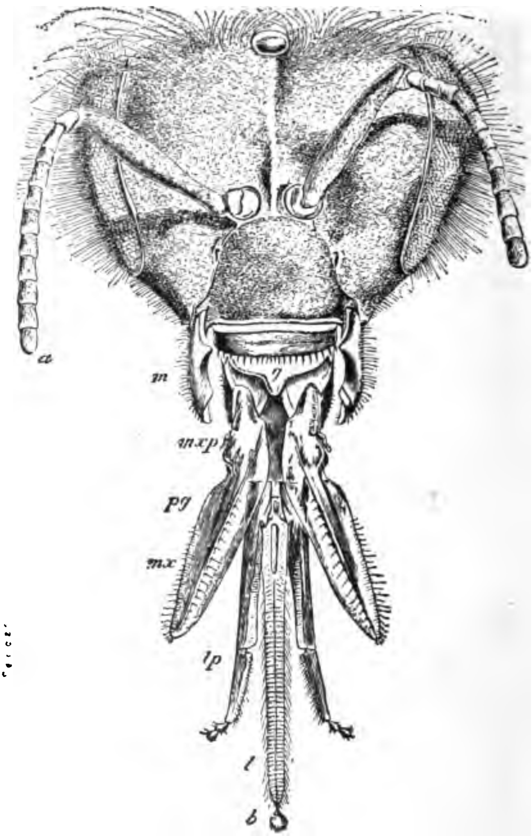


FIG. 129. Head of worker honeybee. *a*, antenna; *b*, bouton; *g*, epipharynx; *m*, mandible; *mx.*, maxilla; *mxp.*, maxillary palpus; *l*, hypopharynx; *lp.*, labial palpus. (From Packard after Cheshire.)

THE HEAD AND ITS APPENDAGES (Fig. 129). — The segments comprising the head can only be distinguished with any degree of accuracy in the embryo, and even there their number is not certainly established. There are probably six. A large part of the head is occupied by the *compound eyes*, one on either side. These differ in size in queen, worker, and drone, but are prominent in all; they will be described in detail later. Besides these there are three simple eyes, the *ocelli*, arranged in a triangle almost directly on top of the head in the queen and worker, and in front just above the antennæ in the drone. Projecting from the front of the head are two feelers or *antennæ* (Fig. 129, *a*) which serve as organs of special sense.

The MOUTH PARTS consist of a labrum or upper lip, the epipharynx (Fig. 129, *g*), a pair of mandibles (*m*), two maxillæ (*mx*), and a labium or under lip (*l*, *lp*.). The *labrum* is joined to a dome-shaped part of the skull, called the *clypeus*, which lies just above it. From beneath the labrum projects the fleshy *epipharynx* (*g*); this is an organ of taste. The *mandibles*, or jaws, are situated one on either side of the labrum; they are notched in the queen and drone, but smooth in the worker. The latter makes use of them in building honeycomb. The *labium* is a complicated median structure extending downward from beneath the labrum. It is joined to the back of the head by a triangular piece, the *submentum*. Next to this is a chitinous, muscle-filled piece, the *mentum*, beyond which is the *ligula*, or tongue (*l*), with one *labial palpus* (*lp*.) on each side. The ligula may be drawn in or extended. It is long and flexible, with a *spoon* or *bouton* (*b*) at the end. Hairs of various kinds are arranged upon it in regular rows; these are used for gathering nectar, and as organs of touch and taste.

The *maxillæ* (Fig. 129, *mx*.), or lower jaws, fit over the mentum on either side. Along their front edges are rows of stiff hairs. *Maxillary palpi* (*mxp*.) are also present. Nectar is collected in the following manner. The maxillæ and the labial palpi form a tube in the center of which the tongue moves backward and forward. When the epipharynx is lowered, a passage is completed

into the œsophagus. The nectar is first collected by the hairs on the ligula; it is then forced upward by the pressing together of the maxillæ and labial palpi.

THE THORAX AND ITS APPENDAGES. — The thorax consists of three segments, each of which bears a pair of legs. The anterior segment is known as the *prothorax*, the middle segment as the *mesothorax*, and the posterior segment, as the *metathorax*. The mesothorax and metathorax each support a pair of *wings*. The segments of the thorax are comparatively large, since they contain the largest and most important muscles of the body. Externally the thorax is covered with flexible branched hairs, which are of use in gathering pollen (Fig. 130).

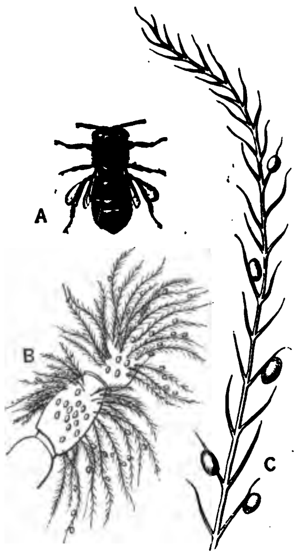


FIG. 130. A, worker honeybee with pollen basket full; B, part of mesothoracic leg with branched hairs and pollen grains; C, one hair bearing pollen grains. (From the Cambridge Natural History.)

LEGS. — Perhaps the most interesting structures of the honeybee are the legs of the worker (Fig. 131). They are wonderfully adapted for the work which they perform. The parts of a typical insect leg, naming them in order beginning at the proximal end, are the *coxa* (*c*), *trochanter* (*tr.*), *femur* (*f*), *tibia* (*ti.*), and five-jointed *tarsus* (*t*).

The *prothoracic* legs (Fig. 131, C) possess the following useful structures. The femur (*f*) and tibia (*ti.*) are clothed with *branched hairs* for gathering pollen. Extending on one side from the distal end of the tibia are a number of curved bristles, the *pollen brush* (*b* in C and E), which are used to brush up the pollen loosened by the coarser spines; on the other side

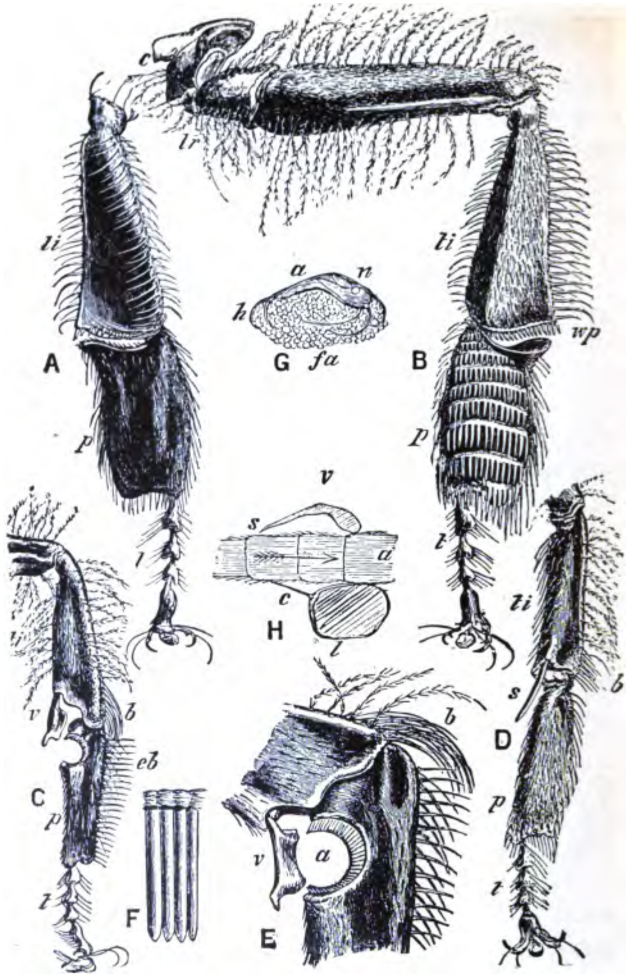


FIG. 131. Legs of worker bee. (After Cheshire.) A, outer side of metathoracic leg: *p*, metatarsus; *t*, tarsus; *ti.*, tibia. B, inner side of metathoracic leg: *c*, coxa; *p*, metatarsus; *t*, tarsus; *ti.*, tibia; *tr.*, trochanter; *wp.*, wax pinchers. C, prothoracic leg: *b*, pollen brush; *eb.*, eye brush; *p*, metatarsus; *t*, tarsus; *ti.*, tibia; *v*, velum. D, mesothoracic leg: lettering as in C; *s*, pollen spur. E, joint of prothoracic leg; lettering as in C. F, teeth of antenna comb. G, cross section of tibia through pollen basket; *fa.*, pollen; *h*, holding hairs; *n*, nerve. H, antenna in process of cleaning; *a*, antenna; *c*, antenna comb; *l*, section of leg; *s*, scraping edge of *v*, velum. (From Root.)

is a flattened movable spine, the *velum* (*v* in C and E) which fits over a curved indentation in the first tarsal joint or metatarsus (*p* in C). This entire structure is called the *antenna cleaner* and the row of teeth (F) which lines the indentation is known as the *antenna comb.* Figure 131, H, shows in section how the antenna (*a*) is cleaned by being pulled between the teeth (*c*) on the metatarsus (*l*) and the edge (*s*) of the velum (*v*). On the front of the metatarsus is a row of spines (*eb.* in C) called the *eye brush,* which is used to brush out any pollen or foreign particles lodged among the hairs on the compound eyes. The last tarsal joint of every leg (Fig. 132) bears a pair of notched *claws* (*an.*) which enable the bee to obtain a foothold on rough surfaces. Between the claws is a fleshy glandular lobule, the *pulvillus* (*pv.*) whose sticky secretion makes it possible for the bee to cling to smooth objects. *Tactile hairs* are also present (*fh.*).

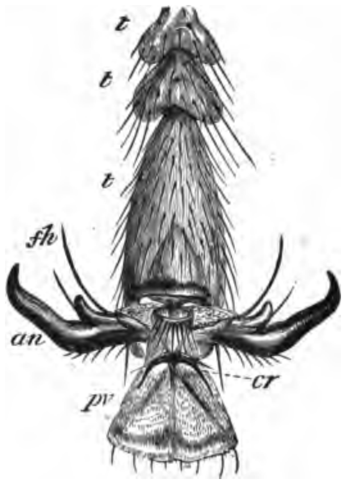


FIG. 132. Foot of honeybee. *an.*, claw; *fh.*, tactile hairs; *pv.*, pulvillus; *t*, tarsal joints. (From Packard after Cheshire.)

The middle, or *mesothoracic legs* (Fig. 131, D) are provided with a *pollen brush* (*b*), but, instead of an antenna cleaner, a *spur* (*s*) is present at the distal end of the tibia. This spur is used to pry the pollen out of the pollen baskets on the third pair of legs, and to clean the wings.

The *metathoracic legs* (Fig. 131, A and B) possess three very remarkable structures, the pollen basket, the wax pinchers (*wp.* in B), and the pollen combs (at *p* in B). The *pollen basket* consists of a concavity in the outer surface of the tibia with rows of curved bristles along the edges (*ti.* in A). By storing pollen

in this basketlike structure, it is possible for the bee to spend more time in the field, and to carry a larger load at each trip. The pollen basket in cross section is shown in Figure 131, G. The *pollen combs* (at *p* in B) serve to fill the baskets by combing out the pollen, which has become entangled in the hairs on the thorax, and transferring it to the concavity in the tibia of the opposite leg. At the distal end of the tibia is a row of wide spines; these are opposed by a smooth plate on the proximal end of the metatarsus. The term *wax pinchers* (*wp.* in B) has been applied to these structures, since they are used to remove the wax plates from the abdomen of the worker.

WALKING. — In walking three legs are extended at one time, the other three supporting the body like a tripod. The foreleg pulls the body forward, the middle leg maintains equilibrium, and the hind leg pushes the insect forward. The details of walking in insects are very complicated.

WINGS. — Each of the first two thoracic segments bears a pair of membranous wings. When at rest the wings lie horizontally over the abdomen, but when flying are widely spread. The wings may be described as transparent membranes supported by hollow ribs called *nerves* or *veins*. The pair of wings on one side of the body may be joined together by a row of *hooklets* on the anterior margin of the hind wing, which are inserted into a *troughlike fold* in the posterior margin of the fore wing.

FLIGHT. — When flying the wings act as inclined planes, and locomotion forward is attained by both up and down strokes, the tips of the wings moving in a curve shaped like a figure 8. Motion backward, or a sudden stop, may be accomplished by changing the inclination of the plane of oscillation.

THE ABDOMEN AND ITS APPENDAGE. — The abdomen is made up of a series of six visible segments or rings of chitin inclosing a large part of the alimentary canal, nervous system, reproductive organs, etc. Each ring has a dorsal plate, the *tergum*, and a ventral plate, the *sternum*. Thin chitinous membranes connect the rings, and make the movement and expansion of the abdomen possible.

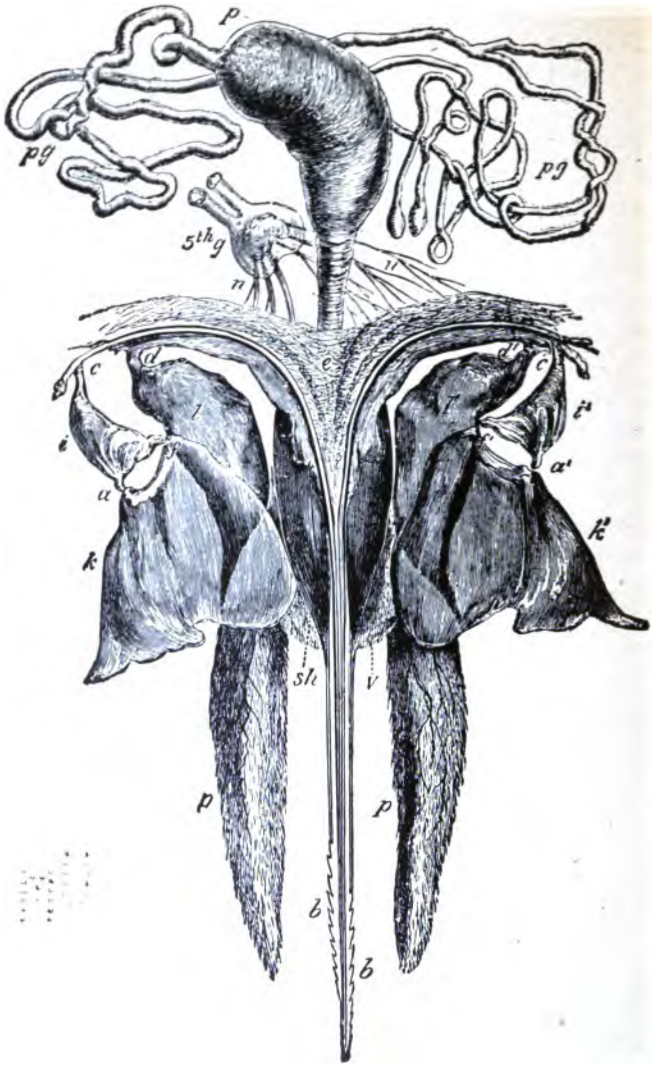


FIG. 133. Sting of the worker bee. *b*, barbs on darts; *i*, *k*, *l*, levers to move darts; *n*, nerves; *p*, sting-feeler; *pg.*, poison gland; *ps.*, poison sac; *sh.*, sheath; *5th*, fifth abdominal ganglion. (From Packard after Cheshire.)

Each of the last four visible sternal plates of the worker bears a pair of *wax glands*. At the end of the abdomen of the worker and queen is the *sting*, and the slitlike openings of the sexual organs and *anus*. There is no sting in the drone, but a *copulatory organ* is present.

THE STING.—The sting is a very complicated structure (Fig. 133). Before the bee stings, a suitable place is selected with the help of the *sting feelers* (*p*); then the two barbed *darts* (*b*) are thrust forward. The *sheath* (*sh.*) serves to guide the darts, to open up the wound, and to aid in conducting the poison. The *poison* is secreted in a pair of glands (*pg.*), one *acid*, the other *alkaline*, and is stored in a *reservoir* (*p.s.*). Generally the sting, poison glands, and part of the intestine are pulled out when a bee stings, so that death ensues after several hours, but if only the sting is lost, the bee is not fatally injured. The queen seldom uses her sting except in combat with other queens.

The Anatomy and Physiology of the Internal Organs.—GENERAL ANATOMY.—Before considering in detail the systems of internal organs and their functions, it may be well to obtain a general view of their morphology, and point out their resemblances to, and differences from, those of the crayfish. Both the bee and the crayfish have a well-developed muscular system, a digestive system composed in the main of similar parts, a dorsal blood vessel and a number of sinuses, a brain dorsally situated in the head, and a median ventral nerve cord. The chief differences are in the excretory and respiratory systems. No green glands nor gills are present in the honeybee, but in their stead are Malpighian tubules and tracheæ. As in the crayfish, the body cavity is not a true cœlom, the cœlom being restricted to the cavities of the reproductive organs.

THE MUSCULAR SYSTEM.—The body of the bee contains an enormous number of muscles; the largest of these are located in the thorax, and are used to move the wings and legs. Other large muscles are connected with the jaws. Usually the muscles are attached directly to the inner surface of the exoskeleton, often

by means of hard tendons. Muscular action is either voluntary or involuntary; for example, the jaws and wings are moved by voluntary, many internal organs by involuntary, muscles. The strength of the muscles of the bee is much greater than that of the muscles of man, compared with their weight. The explanation of this is quite simple, since the weight of a muscle increases as the cube of its diameter, while its strength increases only as the square. A large animal can pull, therefore, comparatively less than a smaller one.

THE DIGESTIVE SYSTEM (Fig. 134).—The digestive canal is made up of the following structures named in order, beginning at the anterior end: the mouth, œsophagus or gullet, honey sac or honey stomach, true stomach, small intestine or ileum, and large intestine or colon. It opens anteriorly by the mouth and posteriorly by the anus. The *œsophagus* (*œs.*) is a narrow tube which passes through the thorax; its posterior end is enlarged into the *honey sac* (*hs.*) situated near the anterior end of the abdomen. At the posterior end of the honey sac is the *stomach-mouth* (*p*); this structure extends slightly forward into the honey sac. It has four triangular lips, which may be opened or closed by two sets of muscles, longitudinal and circular. Near the top of the lips are a number of bristles which project backward. If the alimentary canal of a freshly killed bee is placed in a $\frac{3}{4}$ to $\frac{1}{2}$ per cent salt solution, the lips will open and close rapidly for about half an hour.

The *true stomach* (*c.s.*) is a cylindrical sac; its walls contain a number of circular muscles, and a layer of longitudinal muscles. The digestive juices secreted by its walls change the food into *chyme*. Part of this chyme is absorbed, the rest is forced by muscular contractions into the small intestine. Undigested food is dissolved in the *small intestine*, or ileum (*si.*), and the digested food or chyle is absorbed by its walls. At its posterior end the small intestine gradually merges into an enlargement, the *colon* (*l*). This part of the alimentary canal receives all the undigested matter, and discharges it to the outside through the anus. The

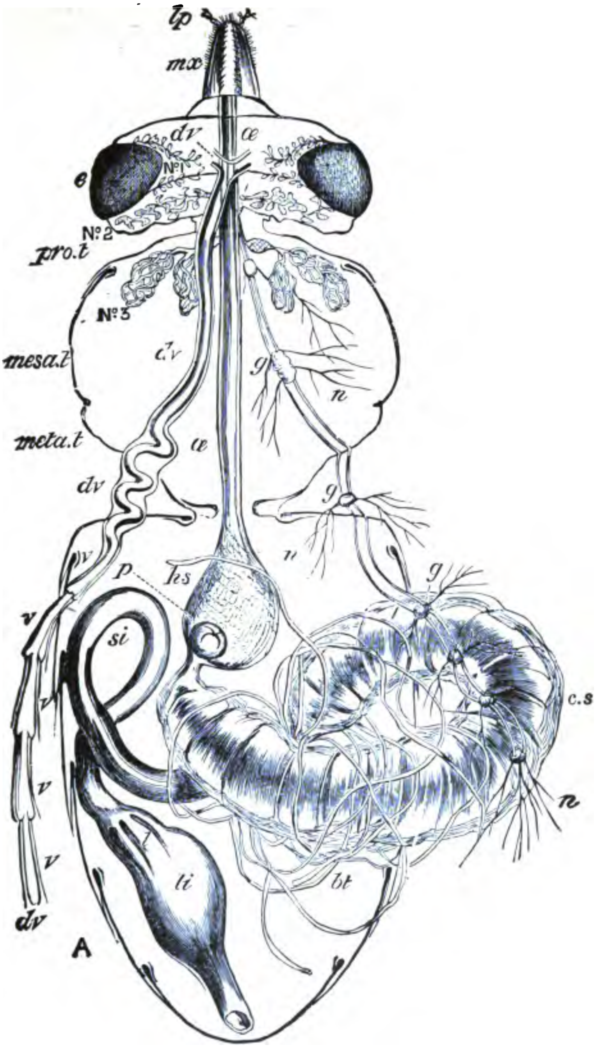


Fig. 134. Internal organs of honeybee. *bt.*, Malpighian tubules; *c.s.*, true stomach; *d.v.*, dorsal vessel; *e*, eye; *g*, ganglia of nerve-chain; *hs.*, honey sac; *li.*, rectum; *lp.*, labial palpus; *mesa. t.*, mesothorax; *meta. t.*, metathorax; *mx.*, maxilla; *n*, nerves; No. 1, No. 2, No. 3, salivary glands; *œs.*, œsophagus; *p*, stomach mouth; *pro. t.*, prothorax; *si.*, small intestine (ileum); *v*, ventricles of dorsal vessel. (From Packard after Cheshire.)

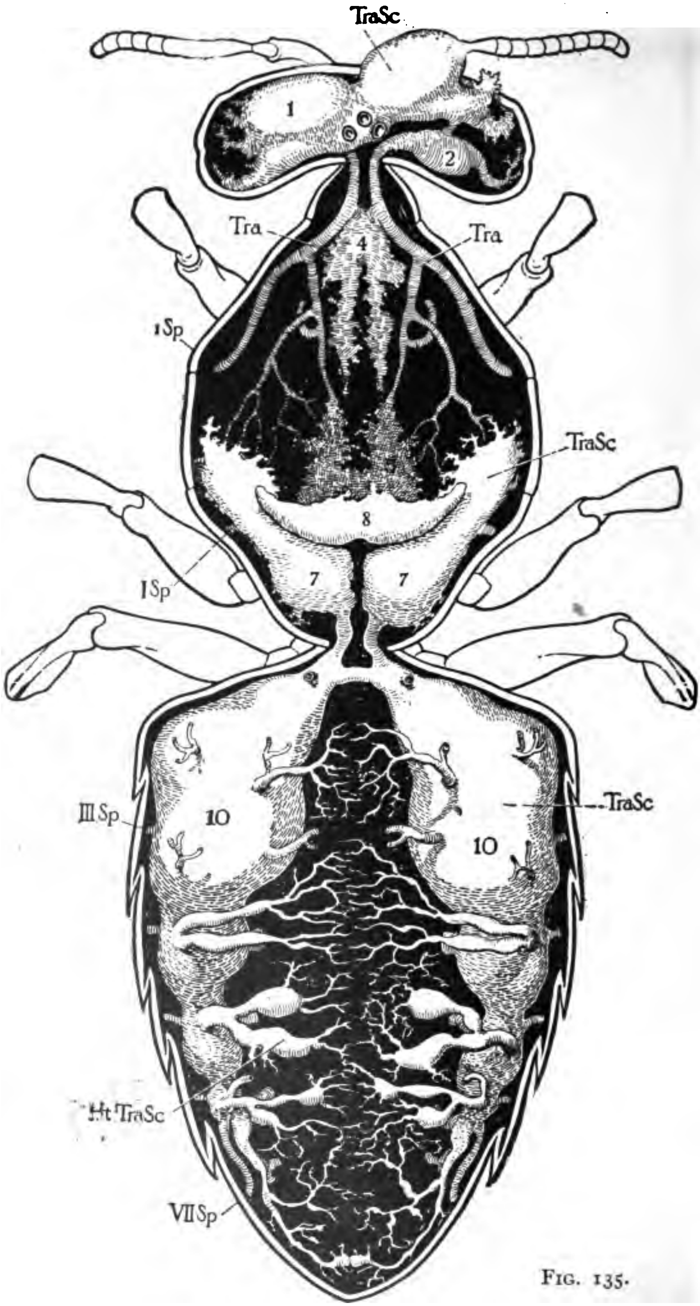
fæces are never voided within the hive if the bees are kept under proper conditions.

THE SALIVARY GLANDS. — There are two pairs of salivary glands, one within the head, the other within the thorax. Those in the head lie against the posterior walls of the cranium. The other pair lie in the ventral part of the anterior half of the thorax. Both pairs of glands produce weakly alkaline secretions which are poured out upon the labium where they act upon the food taken through the proboscis (Snodgrass, 1910).

THE EXCRETORY ORGANS. — The *Malpighian* or *urinary tubules* (Fig. 134, *bt.*) are a number of long, fine, hairlike structures which open into the anterior end of the intestine. They were discovered by and named after the great Italian anatomist Malpighi. Excretions are taken from the blood and the fat body in the form of urates; they pass into the intestine, and thence out of the body.

THE VASCULAR SYSTEM.—The *blood* of the honeybee is similar to that of the crayfish. It is a colorless plasma containing ameboid corpuscles. It differs in one important point from the blood of most other animals — it does not carry very much, if any, oxygen. The distribution of oxygen is accomplished by the respiratory system, as we shall see later.

An even less complete system of *blood vessels* is present than in the crayfish. The principal organ of circulation is the *dorsal vessel*, or *heart* (Fig. 134, *d.v.*). This is a tube lying in the median line just beneath the dorsal surface; it is closed near the posterior end of the abdomen, but opens in the head. The walls of the heart are muscular, and contract at intervals. Blood enters through five pairs of *ostia*, one pair to each of the five compartments or *ventricles* (*v*) into which the heart is divided. *Valves* prevent the flowing back of the blood, so that each contraction sends a stream toward the head. From here it passes through the spaces among the tissues, finally reaching the ventral parts of the body. Beneath the heart is a horizontal diaphragm of muscle, which forms a *pericardial sinus*. By contracting, this diaphragm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1
2
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I Sp
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8
I Sp
7
7
III Sp
10
10
TraSc
Ht TraSc
VII Sp

FIG. 135.

forces the blood from the ventral part of the body into the sinus, and thence through the ostia into the heart.

THE RESPIRATORY SYSTEM (Fig. 135).—The honeybee breathes through openings, called *spiracles* (*sp.*), situated in the sides of certain thoracic and abdominal segments. No air enters through apertures in the head, as in vertebrates. There are two pairs of spiracles in the thorax, one in the sides of the prothorax, the other in the metathorax. Five pairs are present in the abdomen. The spiracles open into tubes, called *tracheæ*. These unite with longitudinal tracheæ which extend along the sides of the body. Other tracheæ arise from these longitudinal trunks and distribute their branches to all parts of the body. The tracheæ (Fig. 136) are tubes composed of a single layer of cells (*a*) and lined with a thin chitinous wall. This wall is thickened at regular intervals, forming a *spiral thread*, which serves to keep the tracheæ open. Certain tracheæ are dilated into *air sacs* (Fig. 135), the largest of which are situated in the anterior part of the

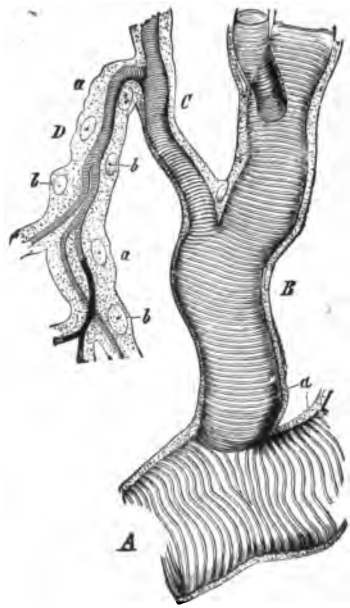


FIG. 136. Portion of a trachea. *a*, cellular wall. (From Packard after Leydig.)

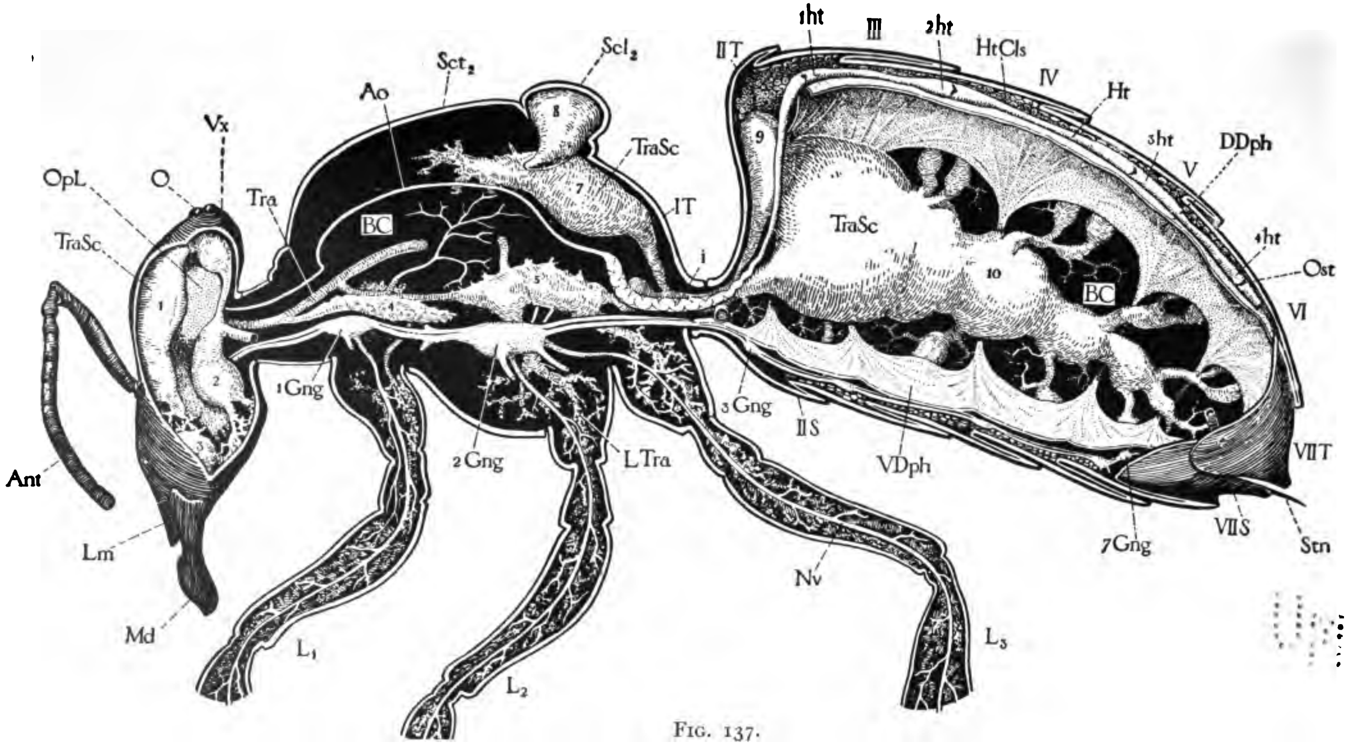
FIG. 135. Respiratory system of worker bee as seen from above, one anterior pair of abdominal sacs removed and transverse ventral commissures of abdomen not shown. *I Sp.*, *III Sp.*, *VII Sp.*, spiracles; *Ht. Tra. Sc.*, *Tra. Sc.*, 1, 2, 4, 7, 8, 10, tracheal sacs; *Tra.*, tracheæ. (From Snodgrass, Technical Series 18, Bureau of Entomology, United States Department of Agriculture.)

abdomen. These are supposed to be of service to the bee during flight, since their size can be increased at will, and the specific gravity of the insect, therefore, decreased. Air is drawn into and expelled from the tracheæ by alternate expansions and contractions of the abdomen. Each spiracle contains a valve, which may be closed or opened. Dust is prevented from entering by hairs which surround the opening.

The *rate* of *respiration* depends upon the activity of the individual. Normally there are about forty inspirations per minute, but in fatigued bees the number reaches as high as one hundred and sixty per minute. The air brought into the bee's body is carried by the tracheæ directly to the tissues, no circulatory system being necessary for the distribution of oxygen.

THE NERVOUS SYSTEM (Fig. 137, *Op. L.–7 Gng.*).—The nervous system of the bee consists of a large chain of paired ganglia and two groups of smaller ganglia, called the stomatogastric, and the sympathetic, respectively. The large ganglionic chain is by far the most important. It is formed of seven masses of nervous tissue, two in the head, two in the thorax, and five in the abdomen. Each mass is composed of two ganglia lying side by side, and connected with the mass in front and behind by two nerve cords. All, except the foremost ganglionic mass, are situated near the center of the ventral body wall. The ganglia at the extreme anterior end occupy a cavity in the dorsal part of the head; they are known as the *brain*, or supraœsophageal ganglia. Nerves connect the brain with the compound eyes (Fig. 137, *Op. L.*), the ocelli, the antennæ, and the labrum. Beneath the œsophagus in the head lies the *subœsophageal ganglion* which innervates the mandibles, labium, and other mouth parts. The *anterior*

FIG. 137. Longitudinal, median, vertical section of entire body of worker bee, showing nervous system (*Op. L.–7 Gng.*), tracheal system (*Tra. Sc.* 1–10), dorsal and ventral diaphragms of abdomen (*D. Dph.* and *V. Dph.*), and dorsal vessel consisting of heart (*Ht.*) and aorta (*Ao.*). (From Snodgrass, Technical Series 18, Bureau of Entomology, United States Department of Agriculture.)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VDph
VIIT
VIIS
Stn
7Gng
Nv
L₁
L₂
L₃

FIG. 137.

ganglion in the *thorax* sends nerves into the front pair of legs. The *posterior thoracic ganglion* is comparatively large, consisting really of several ganglia which have grown together. The anterior part of this ganglion supplies the fore wings and the middle pair of legs; the posterior part innervates the hind wings and legs. Various parts of the abdomen are supplied with nerves from the *abdominal ganglia;* the last of these is larger than the others, because of the important organs, the genital apparatus and the sting, which are innervated by them.

The *stomato-gastric* part of the nervous system is made up of many small ganglia connected with the organs of digestion, circulation, and respiration.

Each segment of the body contains a triangular ganglion from which fine nerve fibers pass to all parts of the body. This is the so-called *sympathetic nervous system.*

THE SENSORY ORGANS.—THE EYES AND VISION.—Each *compound eye* is made up of a great number of long, slender structures called *ommatidia.* There may be as many as five thousand of these in a single eye. The ommatidia are all alike in structure. They may be recognized externally as minute hexagonal areas or facets, among which arise long protective hairs which are unbranched. Passing from without in, the ommatidium is found to contain the following parts: the *cornea;* the *crystalline cone* composed of four modified cells surrounded by two cells containing coloring matter ; and the *rhabdome,* a delicate transparent rod surrounded by eight slender *retinular cells,* and about twelve *pigment cells,* which extend to a *basal membrane.* In all there are twenty-eight parts to each ommatidium (216). The pigment cells prevent the reflection of light within the ommatidium and between neighboring ommatidia.

The *ocelli,* though commonly known as simple eyes, are almost as complex as the compound structures just described. Each ocellus consists of an extremely convex cornea, and a large biconvex crystalline cone, behind which are a great number of rods

resembling somewhat the ommatidia. An optic nerve from the brain passes to each ocellus.

VISION. — A number of interesting biological problems are directly concerned with the vision of the honeybee and other insects; among these may be mentioned the origin of flowers and cross-pollination, the method of finding the way back to the hive, and the finding of the queen by the drone during the nuptial

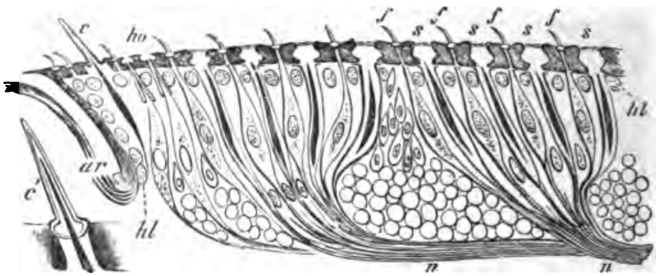


FIG. 138. Longitudinal section through part of an antenna of the honey-bee. *c*, conoid hairs; *f*, tactile hairs; *ho.*, auditory pits; *n*, nerves; *s*, smell hollows. (From Cheshire.)

flight. These questions cannot be definitely answered because the exact character of the image produced by the eyes is not known. A modification of the "mosaic" theory, proposed by Müller in 1826 and described for the compound eye of the crayfish on page 207, is still held by many investigators. Movements are made known to the bee very quickly, according to this theory, and the form of objects while the insect is moving are likewise instantly perceived, since the various facets would be affected in succession.

There is experimental evidence that the ocelli enable the insect to distinguish light from darkness. If images are formed by them, they must be of objects at a definite range, since the lens is incapable of accommodation. Furthermore, the great convexity of the lens makes it probable that form can be perceived

by ocelli at only very short distances, *i.e.* the bee is nearsighted when only the ocelli are used.

SMELL. — There seems to be no doubt but that the principal organs of smell in bees are situated on the antennæ. Other parts of the body also contain organs which have been considered by some to be concerned with the perception of odors. The structures supposed to carry on the function of smell are shown in longitudinal section in Figure 138 at *s*.

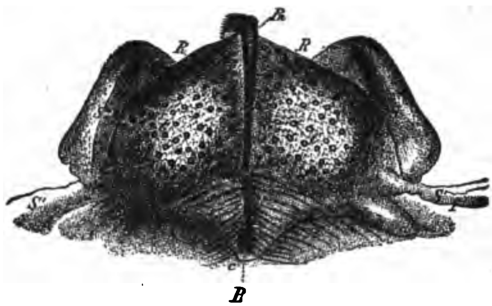


FIG. 139. Taste pits (*R*) on the epipharynx of the honeybee. (From Packard after Wolff.)

They are slight hollows covered by a thin layer of chitin and provided at their bases with a cell supplied with nerve fibers. The number of smell hollows varies for different members of the bee colony; the queen possesses about 1600 on each antenna, the worker 2400, and the drone 37,800. This enormous number on the drone probably aids him in finding the queen during the nuptial flight (198).

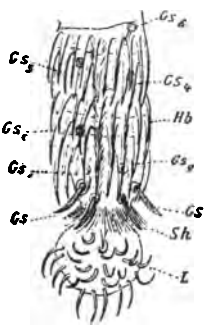


FIG. 140. Taste hairs on tongue of bee. *Gs.*, taste hairs; *L*, bouton. (From Packard after Will.)

TASTE. — Certain structures situated near the mouth of the honeybee have been described as taste organs. The epipharynx (Fig. 139) contains a number of sensory cavities which are considered gustatory by some investigators. Taste setæ are also present near the end of the tongue (Fig. 140, *Gs.*).

HEARING. — The antennæ bear a large number of pits (Fig.

138, *ho.*) supposed to be the end organs of hearing. Each pit has a cone at its base connected with a sensory cell. It is very doubtful, however, whether bees have any sense of hearing, since the exact functions of antennal organs is not known in any case.

The sounds made by bees may be entirely incidental to other activities. Sounds result from the vibration of the wings, the vibration of the abdominal segments, and the activity of the spiracular vocal apparatus. The size of the wings and physiological condition of the bee determine the rate of vibration, and consequently the pitch. When in full flight, the 440 vibrations per second give *a* in the treble clef, but, if fatigued, only 330 vibrations per second may be produced, giving *e*. The so-called *vocal apparatus* lies within the spiracular openings of the respiratory system. It consists of a vocal membrane, a sounding box, and a mechanism for regulating the size of the opening. Air passing to the outside vibrates the membrane producing a humming sound.

Touch. — Bees possess a tactile sense, the end organs of which are hairlike structures on various parts of the body, but especially on the antennæ. At least two kinds of tactile organs occur on the antennæ. One of these consists of a small hair (Fig. 138, *f*) which projects through a minute opening in the chitin, and is connected with a nerve cell (*n*) within. The other touch organs are termed *conoid hairs* (Fig. 138, *c′*); they are larger, and have a central cavity containing a nerve fiber. More tactile hairs are present near the ends of the antennæ than elsewhere.

The Reproductive System. — Male Reproductive Organs (Fig. 141). — In the abdomen of the drone are two *testes* (*Tes.*), each consisting of about three hundred spermatic tubes in which the spermatozoa are formed; they are connected by a pair of fine tubes, the *vasa deferentia* (*V. Def.*), with the *seminal vesicles* (*Ves.*). The seminal vesicles open into a pair of large *mucous glands* (*Ac. Gl.*), which unite at the point where the *ejaculatory duct* (*Ej. D.*)

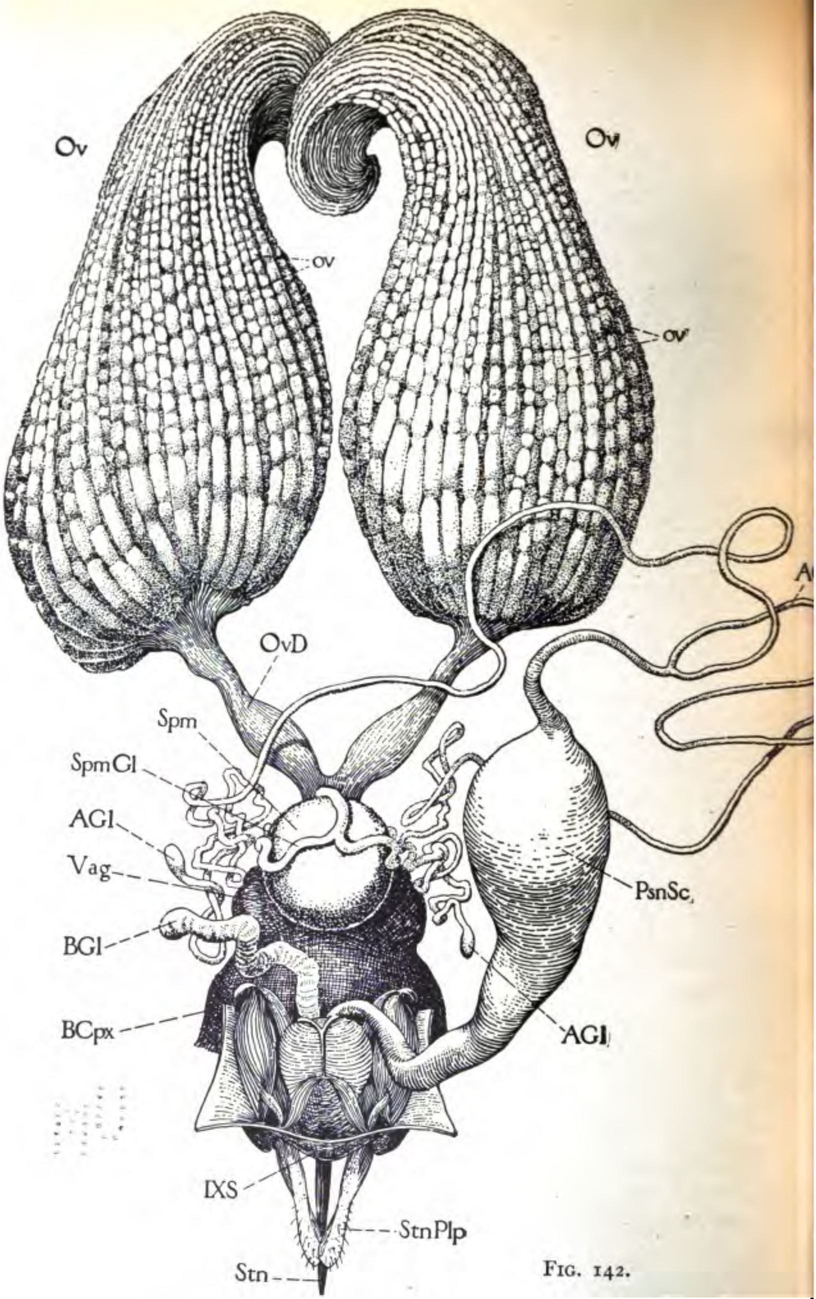

Ov
Ov
ov
ov
OvD
Spm
SpmGl
AGl
Vag
BGl
BCpx
PsnSc
AGl
IXS
StnPlp
Stn

FIG. 142.

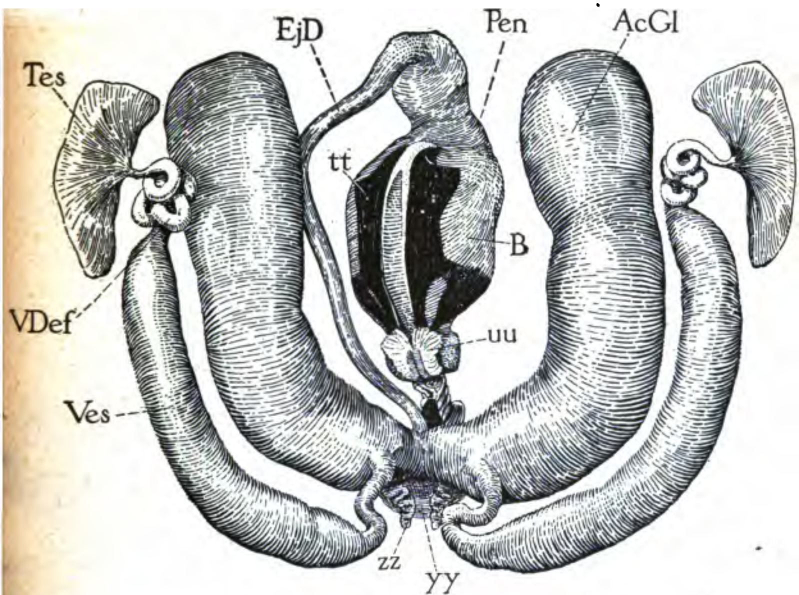


FIG. 141. Reproductive organs of drone bee, dorsal view, natural position. *Ac. Gl.*, accessory gland; *B.*, bulb of penis; *Ej. D.*, ejaculatory duct; *Pen.*, penis; *Tes.*, testis; *V. Def.*, vas deferens; *Ves.*, seminal vesicle; *tt.*, *uu.*, *yy.*, *zz.*, parts of the penis. (From Snodgrass, Technical Series 18, Bureau of Entomology, United States Department of Agriculture.)

begins. At the posterior end, the ejaculatory duct enters the *copulatory organ* (*Pen.*).

FEMALE REPRODUCTIVE ORGANS (Fig. 142). — As stated on page 233, the queen lays all of the eggs, the workers being sexually

FIG. 142. Reproductive organs, sting, and poison gland of queen. *A. Gl.*, acid gland; *A. Gl. D.*, duct of acid gland; *B. Gl.*, alkaline gland; *Ov.*, ovary; *ov.*, ovarian tubule; *Ov. D.*, oviduct; *Psn. Sc.*, poison sac; *Spm.*, spermatheca; *Stn.*, sting; *Stn. Plp.*, sting feeler; *Vag.*, vagina. (From Snodgrass, Technical Series 18, Bureau of Entomology, United States Department of Agriculture.)

undeveloped females. The latter, however, contain vestigial reproductive organs which may even, under certain conditions, become capable of producing eggs. The abdomen of the queen is almost completely filled by the two *ovaries* (Fig. 142, *Ov.*). Each ovary is made up of a great number of *ovarian tubules* (*ov.*) containing eggs of various sizes, the largest at the posterior end. Eggs pass from these tubules into the *oviducts* (*Ov. D.*), thence into the *vagina* (*Vag.*), and out of the body by way of the genital aperture. Opening into the vagina is a spherical sac, the *spermatheca* (*Spm.*), filled with spermatozoa received from the male during copulation.

Spermatogenesis. — The maturation of the male cells of the honeybee differs markedly from the usual type (p. 103), and from that of the animals thus far described. The primordial germ cells grow into spermatogonia as usual. The first spermatocyte division, however, which ordinarily results in two secondary spermatocytes of equal size, is a sort of budding process. A small portion of the cytoplasm is pinched off and disintegrates. The cell remaining, the secondary spermatocyte, retains all of the chromatin originally contained in the spermatogonium. The secondary spermatocyte now divides, producing one small cell with half of the chromatin, but very little cytoplasm, and one large cell. The small cell begins to develop into a spermatozoon, but probably degenerates. The larger cell, which may now be called a spermatid, metamorphoses into a single functional spermatozoon (209, 210).

Oogenesis. — It is now pretty well established that the eggs which produce drones are not fertilized, while those that produce the workers and queens are. The ripening of the latter is similar to this process in other animals, but the maturation of the unfertilized "drone egg" is unique. A full account of this process has been published by Petrunkewitch (215).

Copulation. — The spermatozoa are transferred from the drone to the queen while the latter is taking her nuptial flight. Usually from five to eight days after the queen emerges from her

cell, she ventures out of the hive, first crawling about near the entrance, then taking short flights, and finally her wedding trip of from three to thirty minutes. She is followed by the drones, one of which copulates with her. The result of copulation is the filling of the spermatheca of the queen with spermatozoa (Fig. 143). She usually copulates only once, the sperm obtained at that time being sufficient to fertilize thousands of eggs. After her nuptial flight the queen never leaves the hive except with a swarm.

FIG. 143. Spermatheca of queen honeybee. *a*, space filled with fluid; *b*, mass of spermatozoa; *c*, duct; *d*, active spermatozoa. (From Packard after Cheshire.)

FERTILIZATION. — The eggs are fertilized just before deposition. How this is accomplished is not definitely known. The queen seems to be able to lay fertilized or unfertilized eggs according to the size of the cell in which the individual is to develop, but it has been proven that the size of the cell does not automatically determine this. Fertilized eggs develop into queens and workers, whereas the unfertilized eggs which develop, become drones. The method of control of fertilization is still a mystery.

EGG LAYING. — The eggs are bluish white, and oblong in shape; they are deposited by the queen at the base of the cells and fastened in a position parallel to the sides of the cells by a glutinous secretion. The fertilized eggs are laid either in small worker cells, or in large irregular queen cells. Unfertilized eggs are usually laid in drone cells.

Embryology. — The fertilized egg is made up of a large central mass of *yolk spheres*, among which are traces of *cytoplasm*, and a peripheral layer of cytoplasm. A single nucleus is present; this is the nucleus of the egg and that of the spermatozoon combined. A chitinous shell, the *chorion*, surrounds the egg; this is

lined by a delicate *vitelline membrane*. As in the crayfish, *cleavage* proceeds without the intervention of cell walls. Most of the cleavage nuclei migrate to the periphery, where they form a single layer of cells, the *blastoderm;* the rest remain in the yolk, which it is their duty to change into protoplasm as development continues. The blastoderm soon becomes thicker on one side of the egg, forming the *germ band* or primitive streak. This later becomes

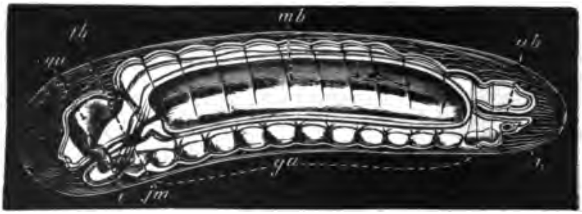


FIG. 144. Embryo of honeybee within eggshell. *ab.*, hind-intestine; *c*, œsophageal connectives; *ch.*, chorion or eggshell; *fb.*, fore-intestine; *ga.*, ganglia; *mb.*, mid-intestine; *s. ga.*, brain. (From Packard after Cheshire.)

the ventral side of the young bee. Next a *median groove* appears in the germ band and two layers of cells arise in this region; the outer layer is the *ectoderm*, the inner, the *entomesoderm*. The latter, as its name implies, gives rise to both the *entoderm* and *mesoderm*. The germ band now grows around the egg until it covers the entire surface. The antennæ and four pairs of appendages appear near the anterior end of the embryo. One pair of the latter disappear; the others become the mouth parts. Three pairs of appendages also develop on the thorax; but disappear before the embryo hatches (200). Some of the organs of the embryo are shown in Figure 144. The ganglia of the brain (*s. ga.*) and ventral nerve cord (*ga.*) are quite distinct at this time, and the three principal parts of the alimentary canal, the *fore-intestine* (*fb.*), *mid-intestine* (*mb.*), and *hind-intestine* (*ab.*) occupy the longitudinal axis of the body.

Metamorphosis.—The life history of an individual may be divided into four periods, *egg*, *larva*, *pupa*, and *adult* or *imago*.

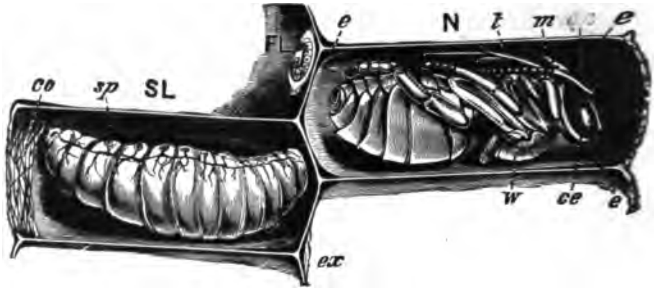


FIG. 145. Larvæ and pupa of honeybee in their cells. *Sl.*, larva spinning cocoon; *N*, pupa; *FL.*, young larva; *an.*, antenna; *ce.*, eye; *co.*, cocoon; *m*, mandible; *sp.*, spiracles; *t*, tongue; *w*, wing. (From Packard after Cheshire.)

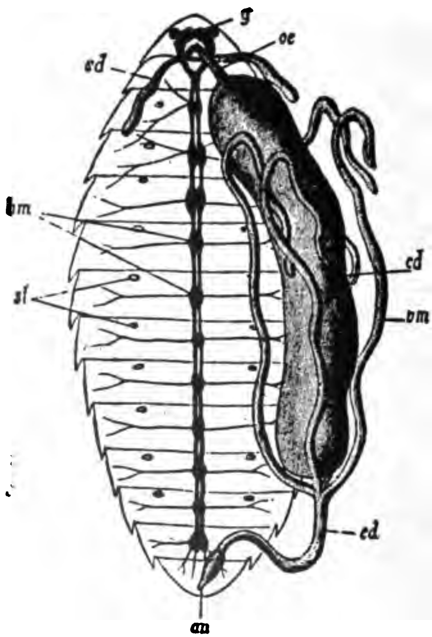


FIG. 146. Internal organs of larval honeybee. *an.*, anus; *bm.*, nerve chain: *cd.*, true stomach; *ed.*, hind-intestine; *g*, brain; *st.*, spiracles; *œ*, œsophagus; *sd.*, spinning gland; *vm.*, Malpighian tubule. (From Packard after Leuckart.)

The length of time of each state is shown in Table XI (191, p. 28).

TABLE XI

THE TIME OCCUPIED IN THE DEVELOPMENT OF QUEEN, WORKER, AND DRONE

	Egg	Larva	Pupa	Total from deposition of egg to adult
	Days	Days	Days	Days
Queen . .	3	5½	7	15½
Worker . .	3	5	13	21
Drone . .	3	6	15	24

After three days the larva emerges from the egg, and lies at the base of the cell (Fig. 145, *FL.*) floating in the food prepared by the workers and known as *chyle* or "bee milk." Chyle is composed of digested honey and pollen, probably mixed with a glandular secretion, and is given to all of the larvæ by the nurse bees during the first three days. Then the larvæ that will become workers are given honey and digested pollen in gradually increasing amounts; the drone larvæ, after the fourth day, also receive honey and undigested pollen; but the queen larvæ are fed lavishly on the rich albuminous bee milk, the "royal jelly," until they change to pupæ.

Growth during the larval period is accompanied by several *moults* of the chitinous larval envelope. At the end of the larval period the cells containing the young brood are covered over with wax, feeding ceases, and the larvæ proceed to spin a *cocoon* of silk from their spinning glands (Fig. 145, *SL.*). These spinning glands (Fig. 146, *sd.*) become the salivary glands (systems I and II) of the adult. The simple structure of the larva is shown in Figure 146. The alimentary canal consists of an *œsophagus* (*œ*), a *chyle stomach* (*cd.*), a *hind-intestine* (*ed.*), and two sets of appendages, the *spinning glands* (*sd.*), and the *Malpighian* tubules (*vm.*). Almost every segment contains a pair of *spiracles* (*st.*), and a *ganglion* of the central nervous system (*bm.*).

It takes the worker thirty-six hours to spin its cocoon, then it slowly changes into a pupa, or chrysalis (Fig. 145, *N*). Practically the entire body is made over at this time; the three regions, head, thorax, and abdomen, become distinct; externally the wings (*w*), legs, mouth parts (*t*, *m*), sting, antennæ (*an.*), and eyes are visible; and the internal changes are even more striking, the larval organs developing into those of the adult, and new organs appearing. After a period of rest the pupa casts off its exoskeleton, and emerges as an adult.

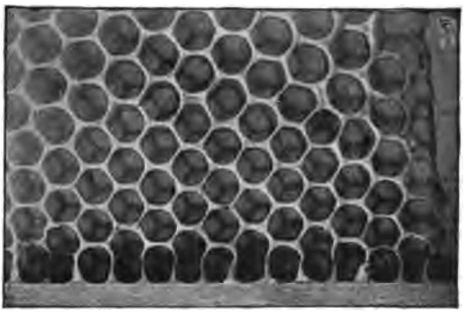
The Activities of the Workers. — The functions of the queen and drone are few as compared with those of the worker. The *queen* lays eggs, and the *drone* fertilizes the queen. But the *workers* have a large number of varied activities, such as the building of honeycomb, the collection of propolis or "bee glue" with which the inside of the hive is varnished, the gathering of pollen or "bee bread" and its preparation as food, the feeding of the queen and young bees, the carrying of water, the collection of flower nectar and its manufacture into honey, and the cleaning, warming, ventilating, and guarding of the hive. Workers also accomplish the pollination of flowers, raise new queens when necessary, and increase the number of colonies by swarming.

THE BUILDING OF HONEYCOMB. — Wax is produced by pairs of wax glands on the sterna of the last four visible abdominal segments of the worker. Honey and pollen are consumed in the process, and a temperature of from 97° to 98° F. is maintained. When comb is to be built, the bees gorge themselves with honey, and hang in dense clusters from the top of the hive for several hours. Thin scales of wax are then secreted by the wax glands, removed by the wax pinchers on the metathoracic legs, transferred to the prothoracic legs, and then to the mouth, where they are mixed with saliva and kneaded by the jaws. If a new comb is to be built, the wax is plastered to the roof, and in some mysterious way each bee puts its contribution almost exactly where it is to remain. The cells, which are gradually built up, are hexagonal in shape.

Cells differ in size according to their uses. There are six kinds — worker, drone, queen, transition, attachment, and honey. The cells in which the *workers* are reared measure one fifth of an inch between the parallel sides. The *drone cells* are larger, measuring one fourth of an inch

Drone cells Transition cells Worker cells

A



B

FIG. 147. Honeycomb showing various kinds of cells. A, diagram showing comparative size of drone cells and worker cells. B, photograph of a piece of honeycomb showing circular cells and attachment cells. (From Root.)

between the parallel sides. At certain times some of the hexagonal cells are torn down and a large *queen cell* is built. Between the worker and drone cells is a zone of irregular *transition cells*. The cells which fasten the comb to the top or sides of the hive are called *attachment cells*. Honey is stored not only in

honey cells, but also in drone, worker, and transition cells. Careful measurements have shown that the cells are seldom perfectly symmetrical, although in many cases they appear so to our eyes. The honey cells are built with entrances slightly above their bases, so that the honey stored in them will not flow out before it becomes "ripe" (200).

THE COLLECTION OF PROPOLIS.—"Bee glue," as propolis is sometimes called, is a resinous material collected from buds and crevices of trees. It is transported in the pollen baskets, and is used, as soon as collected, to paint the inside of the hive, to fill up cracks, and to strengthen any loose parts.

GATHERING POLLEN.—Pollen grains are of inestimable value in the bee household. They are very small, of various shapes and colors, and are formed within a part of the flower, known as the anther. The pollen grains contain the male element in the fertilization of flowers, and consequently are necessary for the production of fertile seed. To the bee, pollen is invaluable as a food, and is also used in preparing the cells containing pupæ. We have already described the peculiar structures on the legs and other parts of the bee's body used in collecting pollen (p. 236). Upon reaching the hive the pellets of pollen are pried out of the pollen basket by the spur at the termination of the tibia of the middle leg (Fig. 131, *D*, *s*), and deposited outside the brood clusters in whatever cells are available—usually in worker cells. Pollen is the principal food of the larvæ. It is very rich in nitrogenous material, a food element not found in honey, and without which the young would starve. The gathering of pollen by bees has a great influence upon the flowers visited, as is explained in another place (p. 262).

CARRYING WATER.—During warm weather water is sucked up into the honey sac from dew, or brooks and pools, and carried to the larvæ in the hive. In cool weather moisture condenses in the hive in sufficient quantities, and, under some conditions, to such an extent as to injure the inhabitants.

THE MANUFACTURE OF HONEY.—Bees do not collect honey from

flowers, but gather nectar, which is later transformed into honey. The nectar is lapped up by the tongue (Fig. 129, *l*), and transferred to the honey sac (Fig. 134, *hs.*), where it is stored while the bee is in the field. Part of the water contained in the nectar may be excreted before the hive is reached. Nectar is placed in open cells in the well-ventilated hive until all but 18 to 20 per cent of the water contained in it has evaporated. When a cell is finally filled with "ripe" honey, it is sealed with a cap of wax.

The flavor of honey depends upon the kind of flowers from which the nectar is collected. "Among the most important producers of the best honey in the East and North are white clover, basswood, buckwheat, and the fruit trees and small fruits; in the middle states are the tulip tree, sorrel tree, sweet clover, and alfalfa; in the South are the mangrove, cabbage and saw palmettos, and sorrel tree; while in the West are alfalfa and white sage. The best and most of the California honey is from the wild white sage" (207, p. 529). The amount of honey produced in one hive in a fair season ranges from an average of about thirty pounds of comb honey to possibly fifty pounds of extracted honey. This will net the beekeeper from ten to fifteen cents per pound (218).

CLEANING THE HIVE. — The health of the swarm depends upon the cleanliness of their domicile, since perfect sanitary conditions are necessary where so many individuals live in such close quarters. Dead bees, pieces of old comb, the excreta of the queen, drones, and others that remain in the hive, and any other waste material is immediately removed.

VENTILATING THE HIVE. — Fresh air for the hive is obtained by the exertions of certain of the workers. Many bees near the entrance, and at other places in the hive, are busily engaged in vibrating their wings, and creating a current of air, which keeps the hive fresh, and aids in ripening the nectar. The loud buzzing which accompanies this activity is often heard at night after a large amount of nectar has been collected (191).

GUARDING THE HIVE. — The hive is guarded against the intru-

sions of yellow jackets, bee moths, and other bees by workers, who wander back and forth near the entrance, and examine every creature that visits the colony. If the swarm is strong, the guards succeed, with the aid of the beekeeper, in warding off all honey-loving enemies.

SWARMING. — The number of bees in a hive increases very rapidly, since the queen usually lays from 950 to 1200 eggs per day. When the colony is in a prosperous condition, and there is danger of overcrowding, queen cells are built by the workers, usually around the fertilized eggs, and new queens are reared. Two queens do not live amicably in one hive, and, if such a condition arises, either there is a battle between the two, resulting in the death of one of them, or the workers kill one, or else the old queen collects from two to twenty thousand workers about her and flies away with them to found a new colony. This is known as swarming. The old hive is not broken up, but continues its existence as before.

Swarming occurs in May, June, or July, according to latitude, and a second swarming period may be inaugurated if weather conditions result in a midsummer flow of honey. Before issuing from the hive, the honey sacs are filled with honey to serve until a new home is found. The swarm, after flying a short distance, comes to rest upon the limb of a tree or other object where it remains sometimes for several hours. A site for the new colony is sometimes chosen by scouting bees several days before the swarm leaves the parent hive. These scouts may also partially prepare the place by cleaning out loose dirt, bark, etc. The usual choice is a hollow tree, such as the wild ancestors of the honeybee inhabited, and henceforth is called a "bee tree." One of the duties of the beekeeper is to hive the swarms before they succeed in escaping to the woods. Swarms may also be formed artificially.

The Enemies of the Honeybee. — Weak or neglected hives may be attacked by the *Bee Moth, Galleria mellonella*, which takes advantage of every opportunity to enter and lay its eggs.

The larvæ feed principally on pollen, and the cocoons and cast-off larval skins in the brood combs. They make burrows in the comb and line them with silk as a protection from the bees.

The *bee louse, Braula cæca,* is parasitic on bees in Mediterranean countries, but thus far has not gained a foothold in America. The bee lice may weaken the queen by sucking the juices from her body. Other insects, such as dragon flies, ants, and wasps, attack bees, especially in tropical and subtropical regions. Spiders frequently capture bees in their webs.

Birds are accused of using honeybees for food, and one species, the *kingbird,* is called the "bee martin," because of its supposed fondness for them. The percentage of honeybees eaten by kingbirds is, however, very small, and amply repaid by the many other insects they devour.

Toads and lizards are important enemies of the honeybee, but should not be destroyed when captured near the hives, since their removal to a safe distance will prevent them from devouring bees and give them a chance to be of benefit by destroying noxious insects. Mice prey upon pollen, honey, and bees during the winter. Hives also need to be protected against rats, skunks, and bears.

Honeybees, in times of a scarcity of pollen and honey, may become robbers, ruthlessly attacking other hives and carrying away the stores contained in them.

The Diseases of Bees. — Bees are subject to several important diseases. Chief among these are European foul brood and American foul brood which are infectious diseases due to bacteria. These microscopic organisms attack the eggs and the tissues of the larvæ. The diseases may spread from hive to hive throughout the apiary. Dysentery must also be guarded against. Improper food and long confinement in the hive are mainly responsible for this affliction.

2. Bees in General

a. Classification of Honeybees

The bees belong, with the ants, wasps, etc., to the order Hymenoptera. In this order are included all insects with four membranous wings, the hind wings being the smaller; with biting and sucking mouth parts; with a sting, piercer, or saw at the end of the abdomen of the female; and with a complete metamorphosis, *i.e.* with larval and pupal stages during development. The honeybee belongs in the family Apidæ, and is the most specialized with regard to its communistic life of any of the group. The species of honeybee found in this country is *Apis mellifica.* A number of other species of honeybees inhabiting Asia and Africa are placed with *mellifica* in the genus *Apis.* The individuals of the species *Apis mellifica* are not all alike in structure, color, or activities. Seven or more races are recognized. The characteristics of the more important races are contrasted in Table XII. The relations of the honeybees to other insects and to each other are shown in outline in Table XIII.

b. Gynandromorphs

A normal colony of honeybees contains, as stated before, a fertilized, egg-laying queen, a number of males or drones, and thousands of sterile females or workers. A number of bees have been discovered which showed male characters in certain parts of the body and female characters in other parts. Abnormal insects of this kind are known as gynandromorphs. Butterflies, ants, and bees appear to be more often afflicted than other insects. The best well-known instance of gynandromorphism occurred in a hive of bees at Eugster and was reported by von Siebolt. This hive contained an Italian queen and German drones. The workers produced by this queen were therefore hybrids. Some of the gynandromorphs in this colony had the anterior end of the body male, the posterior female; others exhibited male characters on the right and female on the left,

TABLE XII

SOME OF THE CHARACTERISTICS OF THE MORE IMPORTANT RACES OF HONEYBEES [1]

Race	Color of Abdomen	Disposition	Quality as a Producer	Cappings of Comb Honey	Remarks
German	Black	Cross	Poor	White	First race introduced into America
Italian	Yellow stripes	Gentle	Best	Fairly White	Most popular race
Carniolan	Gray	Gentle	Good	White	Some advocates in the United States
Caucasian	Yellow Gray	Gentlest Known	Good	White	Recently reintroduced Good for amateurs
Banat	Black	Gentle	Good	White	Recent
Cyprian	Yellow	Vicious	Good	Watery	Now practically abandoned in United States.

[1] From information furnished by Dr. E. F. Phillips.

TABLE XIII

THE RELATIONS OF THE HONEYBEES TO OTHER INSECTS AND TO EACH OTHER

Class		Insecta		
Orders	Diptera (Flies, etc.)	Lepidoptera (Butterflies and Moths)	**Hymenoptera** (Bees, Wasps, Ants, etc.)	etc.
Families	Formicidæ (Ants)	Eumenidæ (Solitary Wasps)	**Apidæ** (Bees)	etc
Genera	Bombus (Bumblebee)	Megachile (Leaf-cutter Bees)	**Apis** (Honeybees)	etc.
Species	Apis indica (East Indian Honeybee)		**Apis mellifica** (Common Honeybee)	etc.
Races	**Carniolans**	**Italians**	**Germans**	etc.

or *vice versa;* still others had male and female characters in different parts of the same organ. The reproductive organs were often partly male and partly female, and their character could not be determined by the external appearance of the gynandromorphs. Various explanations have been offered to account for this peculiar condition, but as yet the data necessary to decide the question have not been furnished.

c. The Relations of Bees to Other Organisms

Charles Darwin in " The Origin of Species " has used the bumblebee to illustrate " how plants and animals, remote in the scale of nature, are bound together by a web of complex relations." He found " that the visits of bees are necessary for the fertilization of some kinds of clover; for instance, twenty heads of Dutch clover (*Trifolium repens*) yielded 2290 seeds, but twenty other heads, protected from bees, produced not one." . . . " Humblebees alone visit red clover, as other bees cannot reach the nectar, — hence we may infer as highly probable, that, if the whole genus of humblebees became extinct or very rare in England, the heart'sease and red clover would become very rare, or wholly disappear. The number of humblebees in any district depends in a great measure upon the number of field mice, which destroy their combs and nests. . . . Now the number of mice is largely dependent, as every one knows, on the number of cats. . . . Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!" (236, p. 65.) The influence of old maids upon the number of cats was suggested by Huxley as an addition to Darwin's illustration.

Bees and Flowers. — CROSS-POLLINATION. — Bees in flying from flower to flower gathering nectar and pollen accomplish what is known as cross-pollination, *i.e.* the pollen from one flower is carried by the bee to another flower. Cross-pollination seems to be of advantage to the seed, since many flowers are structurally

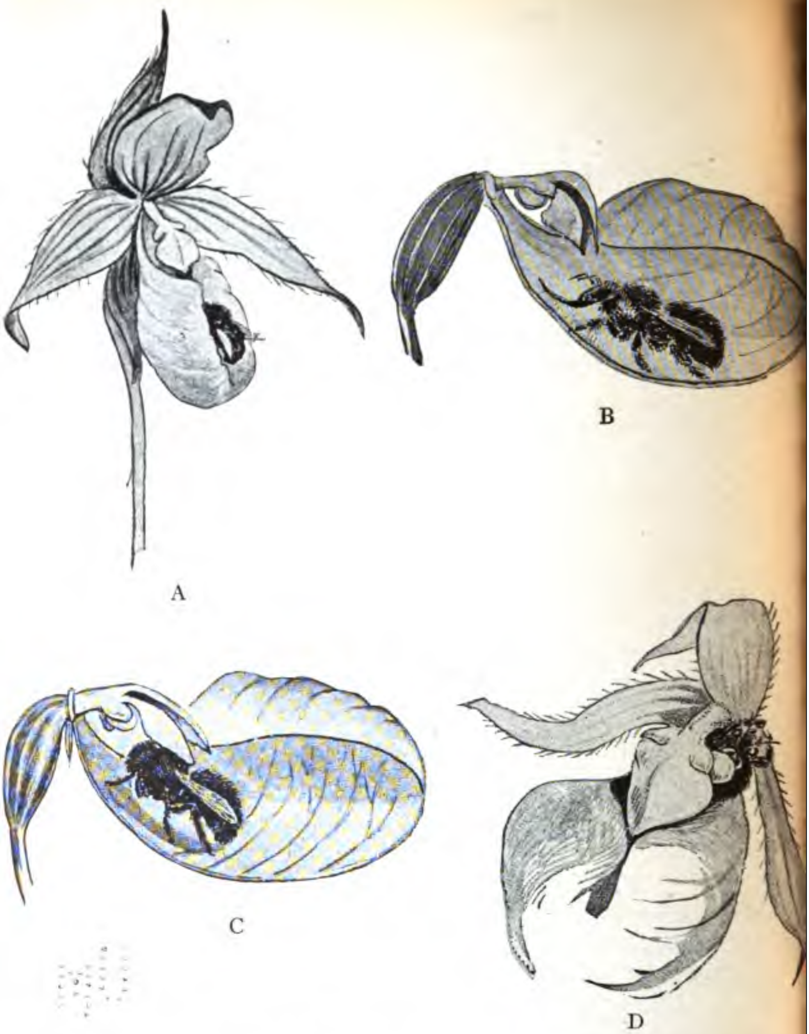


FIG. 148. Pollination of an orchid (*Cypripedium*) by a bumblebee. A, bee forcing i[illegible] way into the flower; B, obtaining nectar within the flower; C, bee escaping brush[illegible] pollen upon the stigma of the flower; before finally escaping the bee receives anoth[illegible] load of pollen from the anther. (From Coulter after Gibson.)

constituted so as to prevent self-pollination and the visitations of unsuitable insects. On the other hand, they are so formed as to secure visits from insects that fly rapidly, and enter many flowers, thus insuring the wide distribution of pollen. The bees are among the most important of the pollinizing insects. They are especially valuable near fruit trees, since it has been demonstrated that orchards containing colonies of bees are more productive than neighboring orchards without bees.

Some of the most interesting arrangements for the securing of cross-pollination are found among the flowers of the orchids. For example, the common lady-slipper (*Cypripedium*) is adapted to the visitations of bumblebees. The flower has a conspicuous pouch with an opening on the upper side of the inner end, over which hangs a flap possessing two anthers and a stigma. The bee forces its way into the pouch (Fig. 148, A) and sucks up the nectar contained within (B). In escaping from the pouch it brushes its back first against the stigma (C) and then against the anther (D). Any pollen present upon the bee's back is brushed off upon the stigma during its escape, and a new supply is then gathered from the anther. The next orchid visited receives this pollen upon its stigma, and adds a new burden to the bee's load. The bumblebee thus is obliged to transfer pollen from one plant to another while gathering nectar (203).

THE COLORS OF FLOWERS. — Many scientists believe that the brilliant colors of many flowers attract bees and other insects, and are therefore instrumental in causing cross-pollination. It is further claimed that the bright colors themselves are the result of the visits of insects, since those flowers that happened to be more brightly colored would be more certain to attract insects, and therefore more liable to be pollinated and produce seed. The selection of the more brightly colored flowers for a sufficient number of years would result in the survival of plants which tend to produce more highly colored flowers. This entire theory of the origin of the colors of flowers because of the visits of insects seems to depend upon the factor that attracts the insect to

the flower. Certain observations apparently prove that smell and not color is the dominant factor (217), whereas other observations have resulted in the conclusion that insects, such as bees and butterflies, that show a high degree of adaptation to flowers, prefer red, purple, and blue, and that insects poorly adapted to flowers favor yellow and white (213). Perhaps the safest view to adopt at present is that color, odor, and structural characters are all important factors influencing the visits of bees and other insects to flowers (204, 208).

d. The Social Life of Bees

Certain species of ants, bees, and wasps exhibit, as in the case of the honeybee, remarkable social organizations. How this has come about is a problem not yet solved, but practically all stages, from a solitary habit to a complex community, are illustrated by various members of the family Apidæ (199, 207).

(1) A SOLITARY BEE. — The leaf-cutter, *Megachile acuta*, is a solitary, long-tongued bee. In building her nest she digs a tunnel, usually in decayed wood, and excavates thimble-shaped cavities in the bottom of it. These cavities are lined with pieces of leaves, generally cut from a rose bush. In the bottom, the bee places a quantity of pollen and nectar, upon which she lays an egg. She then plugs the entrance with pieces of leaves, and flies away. The young that hatch from her eggs live upon the stored food.

(2) A SOLITARY BEE THAT WATCHES ITS YOUNG. — The carpenter bee, *Ceratina dupla*, makes her nest by digging the pith from the center of a dead twig of sumach or other plant. After a long tunnel is excavated she begins at the bottom and constructs a series of chambers with partitions composed of pith. At the bottom of each chamber she places a mass of pollen and lays an egg. She then waits for her offspring to emerge. "The lower one hatches first; and, after it has attained its growth, it tears down the partition above it, and then waits patiently for the one above to do the same. Finally, after the last one in the

top cell has matured, the mother leads forth her full-fledged family in a flight into the sunshine. This is the only case known to the writer where a solitary bee watches her nest till her young mature" (199, p. 669).

(3) SOLITARY BEES WITH A TENDENCY TOWARD A GREGARIOUS HABIT. — Short-tongued bees of the genus *Andrena* are called mining bees, because they dig tunnels in the earth, often more than a foot deep (Fig. 149, B). From the sides of these tunnels

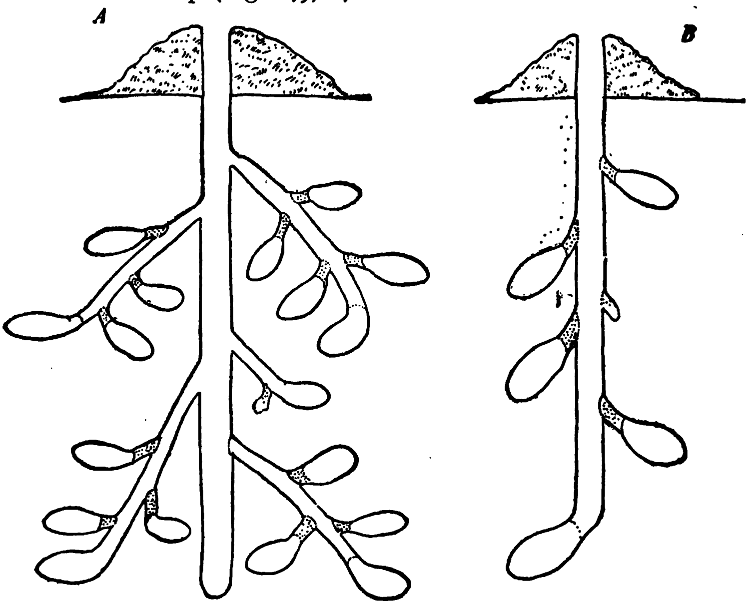


FIG. 149. Diagrams of nest burrows of short-tongued mining bees. A, nest of *Halictus*; B, nest of *Andrena*. (From Kellogg.)

branches lead into cells, in each of which pollen is stored and an egg is laid. The entrance to the cell is then closed. These mining bees seem to enjoy the company of others of their kind, and though each digs her own nest, many tunnels may be placed close to one another, forming villages, sometimes as much as fifteen feet in diameter, and containing over a thousand nests.

(4) Solitary Bees with a Tendency toward Community Life. — The mining bees of the genus *Halictus* make burrows in sand banks and the sides of cliffs (Fig. 149, A). "A remarkable feature in the habits of the bees of this genus is that several females unite in making a burrow into a bank, after which each female makes passages extending sidewise from this main burrow or public corridor to her own cells. While *Andrena* builds villages composed of individual homes, *Halictus* makes cities composed of apartment houses" (199, p. 666).

(5) Social Bees with Annual Colonies. — The bumblebees of the genus *Bombus* form communities composed of queens, males, and workers. Only young fertilized queens survive the winter. In the spring each selects an old deserted field-mouse nest and starts a colony. First a number of workers are reared, being cared for by their mother; these workers then take over the household duties, and the queen devotes herself to laying eggs. As autumn approaches males and queens appear, and finally all perish except the young queens.

(6) Social Bees with Permanent Colonial Life. — The honeybee differs from the bumblebee in many ways. Its life activities are more complex, and its colonies are able to pass the winter without perishing. That their complex community life had evolved from a solitary condition through the stages mentioned above should not be understood, but the life histories of the solitary bees and the bumblebee show many gradations between the strictly solitary life and the complex social lives of these remarkable insects.

FIG. 150. Aristotle, 384–322 B.C. (From Locy.)

CHAPTER XIII

HISTORICAL ZOOLOGY

No one knows when man began to study animal life. The pursuit of certain forms for food, the domestication of others, and the practice of animal sacrifice doubtless furnished some crude and scattered notions of anatomy, physiology, and ecology, even in remote antiquity. The first scientific treatises that had an influence upon modern zoological ideas were not written until about three hundred and fifty years before Christ. At this time Aristotle's works appeared, and so careful were the observations of this remarkable man that they were considered authoritative for twenty centuries.

It is convenient to divide zoological history into five periods: (1) the Greek Period, (2) the Roman Period, (3) the Period of the Middle Ages, (4) the Encyclopedic Period, and (5) the Modern Period.

1. The Greek Period

Aristotle (384–322 B.C., Fig. 150) was the foremost pupil of Plato and the tutor of Alexander the Great. He was early left an orphan with a considerable fortune, and devoted his life to study in a variety of fields. He published three hundred works on philosophy, psychology, rhetoric, and other subjects, but his most important contributions were to natural history, of which science he is justly called the "father." He knew over five hundred species of vertebrates and many invertebrates, and attempted to classify them. His greatest works were on the natural history of animals, the parts of animals, and the development of

animals. They reveal a remarkable familiarity with the facts of comparative anatomy, physiology, and embryology. Aristotle's ideas later furnished the starting point for the founding of our modern systems of classification and theories of evolution, but his greatest contributions to zoology were the methods of work which he introduced. He was a critical compiler, and, from the fabric of scattered facts and fancies which existed at his time, produced a compact and fairly accurate account of animals. He was not content, however, to accept old statements, but verified everything by careful examinations of the animals themselves, and added many new facts.

2. The Roman Period

Pliny (23–79 A.D.) led an active public life under the Roman Empire as a naval commander. His writings consist of thirty-seven volumes, which had a great influence on the ideas of naturalists during succeeding centuries. Unfortunately, they are not critical, combining fact, fable, and fancy in accounts of dragons, gorgons, and other imaginary monsters. As a whole, Pliny's influence was detrimental to zoological progress, and helped inaugurate an era of superstition.

Claudius Galen (130–200 A.D.) was a Greek physician who practiced for a time in Rome. He was the greatest anatomist of antiquity, and his writings remained the best on the subject until the sixteenth century. These works were the results of his own careful studies and dissections of the higher animals, and his descriptions were remarkably clear and forceful.

3. Middle Ages

The Middle Ages are a blank, so far as zoological progress is concerned. Superstition was rampant, and the belief in various fabled animals was prevalent. All zoological questions were referred to the ancient authorities, and original investigation was at a standstill. In one controversy a series of papers was pub-

FIG. 151. Linnæus at Sixty, 1707–1778. (From Locy.)

lished with respect to the number of teeth in a horse's mouth. In this instance not one of the writers seems to have thought of examining an animal, but all were satisfied to quote the words of men who had died centuries before. This intellectual stagnation was primarily due to the fact that all learning was in the hands of the Church, and nothing was considered important except matters pertaining to religion.

4. Encyclopedic Period

Conrad Gesner (1516–1565 A.D.) may be mentioned as one of the best examples of this active but uncritical period. He wrote many works, and his natural history (*Historia Animalium*) was the best work on zoology for a long time. The activities of the naturalists of this period foreshadowed the awakening of ideas which were to throw off the respect for authoritative writings that had hampered the scholars of the Middle Ages.

5. Modern Period

Before the intellectual awakening of the sixteenth century, naturalists essayed to cover the entire field of zoological sciences. The workers of the Modern Period, however, have confined themselves to more limited fields, and certain individuals are responsible in large part for the development of the various subsciences defined in Chapter I. On this account the subjects of systematic zoology, comparative anatomy, histology, embryology, physiology, and evolutionary zoology are considered separately in the following pages.

a. Systematic Zoology

Before the time of John Ray (1629–1705) there had been no very definite idea of a species as such. Ray originated the modern idea of a species, and defined it as the offspring of similar parents. He published several lists of careful descriptions of the species

with which he was familiar, together with a system of classification. Thus the way was cleared for the greatest worker in this field, Carl Linnæus (1707–1778, Fig. 151), who attempted to describe all the existing species of animals and plants. He succeeded in listing 4378 in the tenth edition of his greatest work, *Systema Naturæ*. His great influence, and the wide recognition which was accorded his work, made the systematic side of zoology the most active field of investigation for a long time after his death. The aim of the systematic zoologist has been to describe all the species of animals, and to arrange them according to a natural system, *i.e.* a system that will show their true relationships to one another.

b. Comparative Anatomy

Anatomy up to the sixteenth century consisted in descriptions of the structure of single animals. The points of resemblance of different animals finally led zoologists to compare the anatomy of one with another. The French scientist Cuvier (1769–1832, Fig. 152), may, however, be considered the founder of this branch of zoology, since he extended his studies over the entire animal kingdom, and added a great mass of personal observations to the many descriptions published by his predecessors. Besides a number of treatises on comparative anatomy, he wrote a book on the fossil remains of animals which founded the science of vertebrate paleontology.

Among Cuvier's more noted successors were the Englishmen, Richard Owen (1804–1892) and Thomas H. Huxley (1825–1895), and the American, E. D. Cope (1840–1897). To Richard Owen we owe the introduction of the ideas of analogy and homology. His work on the comparative anatomy of vertebrates has been of great service ever since its publication. Although Huxley made many investigations and published a number of papers on the comparative anatomy of animals, he is best known because of his influence in popularizing zoology. Cope played an impor-

FIG. 152. Cuvier, 1769–1832. (From Locy.)

Fig. 153. William Harvey, 1578–1667. (From Locy.)

tant rôle in the advancement of his chosen field of work. He not only studied living forms, but was one of the greatest contributors to the science of paleontology.

c. Histology

Bichat (1771–1801) was the founder of histology. His work was of a high order, ranking with that of the physiologist J. Müller and the embryologists Van Baer and Balfour. He directed the attention of biologists to the study of tissues, and, though he did not use a microscope and failed to make out the cellular structures, his investigations led to the modern science of histology.

The introduction of the microscope added new impetus to the science of the anatomy of tissues, and resulted in the announcement of the cell theory by Schwann in 1839, as described in Chapter III (pp. 35–36). Max Schultze (1825–1874), by identifying vegetable protoplasm with animal sarcode, reformed the ideas regarding cells. Rudolph Virchow (1821–1903) took up the study of diseased tissues, and helped establish the cell theory as it is understood to-day.

d. Embryology

The rise of embryology dates from the time of William Harvey (1578–1667, Fig. 153) and Marcello Malpighi (1628–1694). The former published in 1651 a work descriptive of the embryology of the chick, and of several mammals. Malpighi was further removed from the influence of the ancients than Harvey, and his works on embryology are of greater value. His contributions include a detailed description of the development of the chick, illustrated by excellent drawings.

Previous to the time of Friedrich K. Wolff, embryologists believed in what is known as the preformation theory. According to this theory the embryo exists in miniature within the egg, and during development simply unfolds and expands. From

this theory grew the idea of encasement, *i.e.* the preformed embryo must contain a second smaller miniature, and this another *ad infinitum*, just as a series of boxes may be made to fit within one another. Wolff did more than any other embryologist to overthrow the preformation theory and to introduce in its stead the idea of epigenesis. By epigenesis Wolff meant the gradual formation of organs from an unorganized egg. The establishment of this theory changed all subsequent work in embryology.

Karl E. von Baer (1792–1876, Fig. 154) was the greatest of all embryologists. His most important services were (1) the excellence of his work, which raised the standard of embryological investigations, (2) the establishment of the germ-layer theory, and (3) the broadening of the field of embryology by making it comparative. He is now known as the "father of modern embryology." Francis M. Balfour (1851–1882) in 1880–1881 published his *Comparative Embryology*. This work is a summary of the enormous literature on the subject that had accumulated during the period inaugurated by von Baer. It also contains the result of much original research and many broad generalizations.

e. Physiology

The medical men of ancient times depended largely upon the investigations of Galen. Diseases were supposed to be due to the presence of spirits and humors in the body. This idea, called the pneuma-theory, was not overthrown until the Revival of Learning. The names of William Harvey (1578–1667), Albrecht Haller (1708–1777), and Johannes Müller (1801–1858) are among the most famous in the field of physiology. Harvey demonstrated the connections between arteries and veins, and discovered the circulation of the blood. Although these contributions to knowledge have made his name famous, the introduction by him of experimental methods in physiological investigations have had a more profound influence upon the progress of physiology.

Haller separated the study of physiology from medicine and

FIG. 154. Karl Ernst von Baer, 1792–1876. (From Locy.)

Fig. 155. Johannes Müller, 1801–1858. (From Locy.)

anatomy, and, in his *Elements of Physiology* (1758), summed up the principal facts and theories of his predecessors. Johannes Müller (Fig. 155) founded modern comparative physiology, and prepared a handbook of the physiology of man, based upon the personally verified statements of others and upon his own observations, which to this day has no equal. He made use of the microscope, and brought to his work a knowledge of physics, chemistry, and psychology. Since his time physiological investigations have progressed along physical and chemical lines, and vital activities are now explained by many in physico-chemical terms.

f. Evolutionary Zoology

It is difficult in this place to give an adequate history of evolutionary zoology without discussing the evolution theory in detail. We shall, however, leave that for the succeeding chapter, and restrict ourselves to a brief account of the work of a very few men who have accomplished the most in this field. Lamarck (1774–1829) was one of the first to recognize the instability of species, and was the first to make use of a genealogical tree to show the relationships of animals. His most important work is entitled *Philosophie Zoologique*, published in 1809. It contains statements of his belief in the inheritance of acquired characters, the result of use and disuse, and other less important views.

But the greatest of all scientists who influence our evolutionary ideas was Charles Darwin (1809–1882, Fig. 156). His book on the origin of species, published in 1859, changed the trend of investigations in many fields of science, and did more than any other factor to place evolution upon a firm foundation. At the present time organic evolution, or the transmutation of species, is accepted by practically every well-known zoologist, and our attention is directed toward the problem of the method by which evolution takes place. Darwin's theories have been assailed frequently, and are no more accepted by many zoologists in

their original form, though they continue to exert an important influence upon many lines of research.

Some of the more recent workers in this field are Me Weismann, and de Vries. Gregor Mendel (1822–1884) wa Austrian monk whose results from a study of the cross different kinds of peas and other plants have given us one few laws of heredity. An account of his work will be fo Chapter XIV (p. 289). August Weismann (born 1834) ardent supporter of Darwinism. He is the foremost living lutionary zoologist. Hugo de Vries has recently brought a work entitled *Die Mutationstheorie*, published in 1901, combats Darwin's theories of the origin of species, and in its stead the "mutation theory," a discussion of wh reserved for the next chapter.

g. Zoology of To-day

As the facts of zoological sciences have increased in num the fields of work have become more numerous and narrower investigations are now carried on by more improved methods in greater detail than ever before. Morphological studies being supplemented by experimental investigations in emb ogy, regeneration, heredity, evolution, and other sciences. mal behavior is one of the most favored subjects of research, is rapidly leading psychologists to a better understanding of animal mind.

Zoology at the present time presents a rich field for origi research. Many of the apparently simple "laws" have b found on close examination to be really very complex. All li of experimental work offer large rewards for the student and op up for him a countless number of fascinating problems.

FIG. 156. Charles Darwin, 1809–1882. (From Locy.)

CHAPTER XIV

GENERAL CONSIDERATIONS OF ZOOLOGICAL FACTS AND THEORIES[1]

1. Heredity and Evolution

a. Facts

(1) The Distribution of Animals in Space — Zoogeography

The earth's surface has an area of about two hundred million square miles, five eighths of which is covered by the sea. This vast territory is not uniform, but presents a great number of sets of conditions. The major habitats are the solid earth, the liquids upon the earth, and the atmosphere. Since protoplasm is impressionable and retains impressions, organisms are modified by and adjusted to these different conditions; *e.g.* *Paramecia* in water of a certain kind, the earthworm in ground that is not too sandy, and the honeybee in the air near flowering plants. The facts of zoogeography have led to the formulation of the three following laws: (1) the law of definite habitats, (2) the law of dispersion, and (3) the law of barriers and highways.

The Law of Definite Habitats. — Among the most important physical factors that determine the habitat of an animal are temperature, water, density, light, molar agents, and food. The

[1] The author realizes the difficulty of doing justice to the facts and theories of evolution and heredity, the social life of animals, reflexes, instincts, and the animal mind in one short chapter; nevertheless, he has endeavored to give a concise account of these subjects, believing that the majority of students who take the introductory course in biology do not continue with the more advanced courses and therefore have no other opportunity of becoming acquainted with this important phase of zoology. No doubt in many cases the aid of a teacher will be necessary for a clear understanding of the subjects treated.

continent of North America has been divided by scientists into definite regions, according to the sum total of the temperature during the season of growth; and regions of a certain temperature, though widely separated, are liable to support similar faunas (255). Winter is met by northern animals in one of four ways: (1) by dying, *e.g.* adult butterflies, (2) migrating, *e.g.* birds, (3) hibernating, *e.g.* bears, (4) remaining active, *e.g.* rabbits. Animals living in tropical regions pass the summer in many cases in a torpid condition, and are said to be æstivating.

A certain amount of water is necessary for life, as the bodies of animals are made up of from 55 to 95 per cent water. In dry climates animals have thick skins, and thus evaporation is prevented. Aquatic animals obtain air from water, as do also some terrestrial species, *e.g.* the earthworm. The density of the water and its salinity determine the distribution of many aquatic organisms.

Light, as we have seen, plays a leading rôle in the lives of animals; many species require it (*Euglena*), but others shun it as much as possible (crayfish), principally in order to escape their enemies. Molar agents, such as currents, limit the number of species and individuals, especially where they act with much force. And finally, food conditions are most effective, since carnivorous animals, *e.g.* lions, must live where they may obtain flesh, herbivorous animals, *e.g.* deer, must live where suitable vegetation abounds, and omnivorous animals, *e.g.* crayfishes, where both flesh and vegetation of certain sorts exist. Table XIV presents roughly the four principal kinds of fauna, and their modes of existence.

The general statement may be made that the major habitats are broken up into minor habitats by variations in the conditions, and the constitution of the organism. There are great differences in the exactness with which the different forms are confined to different sets of environmental conditions. This will be better understood after the other laws of distribution have been discussed.

TABLE XIV

THE FOUR KINDS OF FAUNA AND THEIR MODES OF EXISTENCE

FAUNA	HABITAT	FACTORS OF HABITAT	EXAMPLES
Halobios	Marine	Water { Density, Darkness, Molar agents	Lobster Whale *Grantia*
Limnobios	Fresh water	Water { Density, Darkness, Molar agents	Crayfish *Paramecium* *Hydra* *Planaria*
Geobios	Aerial Terrestrial	Dry, light, low specific gravity	Honeybee Birds Squirrels
	Subterrestrial	Thigmotaxis, darkness	Mole Earthworm
Biobios	Parasitic	Fluid food, darkness	*Ascaris* *Plasmodium*

THE LAW OF DISPERSION. — Animals tend to migrate from the region of their origin. The reason for this is in dispute at the present time. It has been held for many years that every animal produces a greater number of offspring than can be supported in its particular habitat, and, since parents and offspring cannot occupy the same area, some individuals must either migrate or die. There are many scientists, on the other hand, who believe that no overcrowding takes place, but that dispersion is the result of a search for food.

Each species of animal is supposed to have originated in a definite region of the earth's surface, and to have migrated in various directions, enlarging its habitat year by year until an approxi-

mately permanent area is occupied. The region from which migration took place is termed the center of dispersal. The following criteria have been given to determine the center of dispersal of a species: the abundance and size of individuals, the location of closely related forms, and the migration routes now selected by the species (225).

THE LAW OF BARRIERS AND HIGHWAYS.—Animals are confined to certain habitats by barriers. They are prevented from gaining access to a new region by the change in the media, by dearth of food, and the interference of other animals. Common barriers are mountains, bodies of water, open country for forest animals, and forests for prairie-inhabiting species. For example, the crayfish, *Cambarus*, migrates up and down streams, but cannot travel overland to neighboring streams, the honeybee cannot fly across the ocean, nor can *Hydra* enter the sea.

The reverse of a barrier is a highway. Apparently there are routes of migration which are especially favored. This may be illustrated by the flight of birds southward in the autumn, and northward again the following spring. Many birds migrate up and down the Mississippi Valley, and along the Atlantic coastal plain.

COSMOPOLITAN GROUPS OF ANIMALS.—Some species of animals have wide ranges, *e.g.* some are found inhabiting practically every large land area on the earth's surface. Sixteen families of birds, including doves, owls, and ducks, and one family of mammals, the bats, are cosmopolitan groups. Doubtless the wings of the birds have facilitated their dispersal, since they give them remarkable powers of locomotion.

RESTRICTED GROUPS OF ANIMALS.—In a number of cases certain species are restricted to very limited areas. The mountain goat is found only in the higher Rocky and Cascade mountains to Alaska. Islands are famous for the presence of restricted species. Darwin's descriptions of the animals he found in the Galapagos Islands read like fairy tales (235).

DISCONTINUOUS DISTRIBUTION.—Whenever a species occurs in

two widely separated regions, it is safe to conclude that the distribution must once have been continuous. Examples of discontinuously distributed animals are rare. Tapirs inhabit tropical America and the Malay Archipelago; the reed bunting in England reappears in Japan; the white mountain butterfly inhabits the Rocky Mountains of British Columbia and the region of Hudson's Bay, but is absent between these localities.

General Conclusions.—"The laws governing the distribution of animals are reducible to three very simple propositions. Every species of animal is found in every part of the earth having conditions suitable for its maintenance, unless:—

"(*a*) Its individuals have been unable to reach this region, through barriers of some sort; or

"(*b*) Having reached it, the species is unable to maintain itself, through lack of capacity for adaptation, through severity of competition with other forms, or through destructive conditions of environment; or

"(*c*) Having entered and maintained itself, it has become so altered in the process of adaptation [or as a result of other processes] as to become a species distinct from the original type" (249, p. 314).

(2) The Distribution of Animals in Time

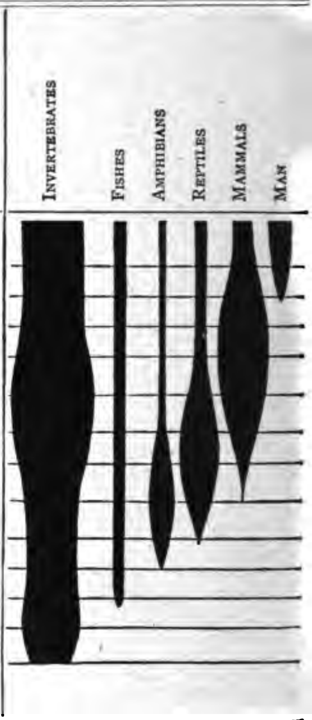
The fossil remains of animals that lived millions of years ago give us authentic records of the fauna present upon the earth's surface at that time. These records, unfortunately, are fragmentary, since only the hard parts of the animals were preserved, and these, when discovered, are almost always broken and incomplete, making the reconstruction of many parts necessary. The number of species of fossil forms known at the present time is given in parentheses after the descriptions of the phyla of the animal kingdom in Chapter I (p. 5). From the evidence obtained from fossils, paleozoologists have constructed a table (Table XV) showing the geological periods, arranged in the

order of their succession, and the time of origin and relative number of the different groups of animals (279).

TABLE XV

THE GEOLOGICAL PERIODS AND THE ORIGIN AND RELATIVE NUMBER OF THE DIFFERENT GROUPS OF ANIMALS

Era	Period	Percentage Duration according to Williams	Duration in Years according to Walcott
Cenozoic	Recent Pleistocene	5	3,000,000
	Pliocene Miocene Eocene	10	
Mesozoic	Cretaceous	10	7,200,000
	Jurassic	5	
	Triassic	5	
Paleozoic	Permian Carboniferous	15	17,500,000
	Devonian	15	
	Silurian	20	
	Cambrian	15	
Archæan	Laurentian		



(3) Variations in Animals

We have already noted (p. 79) that no two organisms are ever exactly alike. In other words, individuals of different species are so dissimilar as to be in most cases easily recognized. Indi-

viduals of the same species, if examined closely, will also be found to vary in certain respects; and even the offspring of the same parents differ from one another to a greater or less degree. The difference between child and parent and between children is called variation. Variations are important in any discussion of evolution and heredity, since their origin and influence upon the transmutation of species constitute the fundamental problems that are occupying the attention of philosophical zoologists at the present time.

CONTINUOUS OR FLUCTUATING VARIATIONS. — If a hundred men are gathered at random, and arranged in a row according to their heights, it will be found that they decrease gradually from the tallest at one end to the shortest at the other. This is an illustration of continuous variation. If now we examine this line more closely, we will find that the greatest number measure about sixty-five inches in height, and that the number of any height decreases as the ends of the line are approached. The measurements decrease or increase gradually from the central mean to one end or the other, and as many variations will be found above the mean as below. The offspring of any of the individuals selected will show a variability that is similarly fluctuating, and follows the law of probabilities. This law holds that slight modifications from the mean are most abundant, and that the greater the variation, and the nearer the extremes are approached, the less numerous the modifications become.

DISCONTINUOUS VARIATIONS. — Animals known as "sports," "saltations," or "mutations" are examples of discontinuous variability. These differ from continuous variations in that they are able to transmit their differences from the mean to their descendants. Some of the most noted sudden variations are the hornless cattle of Paraguay, the niata breed of oxen of South America, and the mauchamp and ancon sheep. The last-named originated from a ram with crooked legs and a long back, that was born in Massachusetts in 1791. When crossed with common sheep, his peculiar characteristics reappeared in the offspring,

and by interbreeding the individuals that showed these traits the ancon race of sheep was established (260). The most famous discontinuous variations known in the plant kingdom are the distinct species of evening primroses, which have originated in recent years from the common primrose, and have been so well described by the Dutch naturalist de Vries (272).

(4) Adaptations of Animals

The adaptations of animals to their environment is so usual as to pass unnoticed. Each of the types we have studied is fitted for life in its particular habitat, and in most cases in no other, a fact which, as we have seen, accounts largely for the geographical distribution of organisms. Animals not only are adjusted to their surroundings, but possess structures which serve them in obtaining food, in defending themselves and their young, and in maintaining supremacy among individuals of their kind. The crayfish is adapted to its environment by the possession of gills for breathing, eyes for detecting moving objects in the water, a hard exoskeleton to protect it from various enemies, pinchers for offense and defense, and a positive thigmotropic reaction which causes it to seek a dark spot out of range of marauders.

Insects are especially favorable for illustrating adaptations. The following structures of the honeybee are excellent examples of adaptations: the hairs and legs for gathering pollen, the alimentary canal for obtaining and storing nectar, the mandibles for molding wax, the sting for self-defense, for the defense of the hive, and, in the case of the queen, for use in determining her supremacy. The origin of adaptations is a moot question among biologists. They are variations which have been inherited, and have become more pronounced in the course of countless generations.

(5) The Struggle for Existence

It has been estimated that if it were possible for oysters to breed unmolested by their enemies, the ocean would be a solid mass of bivalves in four years. Again, if a pair of common robins, which rear on an average four young per year, were allowed to live and produce young year after year, and if all of the offspring were also allowed to live and produce young, the descendants of the first pair would total over one hundred thousand at the end of the tenth year, and over twenty billion at the end of the twentieth year, as shown in Table XVI (256).

TABLE XVI

THE YEARLY INCREASE IN THE NUMBER OF ROBINS IF ALLOWED TO BREED UNMOLESTED

Number of Year	Number of Adults at Beginning of Year	Number of Breeding Pairs of Adults	Number of Young Reared
1	2	1	4
2	6	3	12
3	18	9	36
4	54	27	108
5	162	81	324
6	486	243	972
7	1458	729	2916
8	4374	2187	8748
9	13122	6561	26244
10	39366	19683	78732

Number of robins at end of 10th year 118,098
Number of robins at end of 20th year 20,913,948,846

What really happens, however, is that a few of the birds may succeed in establishing themselves in neighboring regions, but most of the others perish. The final result is a state of practical equilibrium between the number of robins and the factors that

influence their life activities, so that we are able to see very little if any increase, but even a possible decrease, in the number of birds that greet us with the coming of each spring.

These animals are not peculiar in any way, since any species that might be selected would soon cover the earth with its descendants if allowed to reproduce unchecked. In most cases the number of individuals of a species is practically constant from year to year. This is the result of the struggle for existence. An animal must contend with its surroundings; *Euglena* must have light to carry on its life processes; and the honeybee must store up provisions and make its hive secure in order to survive the winter.

The habitat of a species is never large enough to accommodate all the individuals of a species, and an animal is forced to battle for life against others of its kind. The stronger, other things being equal, always wins in the struggle, in other words, the fittest survives. For example, in poor seasons for gathering honey, bees from one hive attack those of another, and, in many cases, carry off the pollen and honey, leaving their victims to starve. Other battles occur between individuals of different species. Whatever the cause of the struggle, it is always the weakest that is vanquished. The strongest individuals of a species live on and keep up the vigor of the race, this being one of the advantages of the elimination of the unfit.

(6) **Heredity**

Heredity has been defined (p. 79) as the " resemblance of child to parent." " A character may be said to be inherited when it always, in one generation after another, is one of the characters of the species, . . . " (269, p. 15). The characters of an organism depend on the nature of its surroundings, especially during development, and on the constitution of the part of the parent from which it grew. In Metazoons this may be a bud, as in *Hydra*, or an unfertilized egg cell, as in the drone bee, but is usually an egg fertilized by a sperm.

We may study inheritance by examining the germ cells, by compiling statistics, or by the experimental method of cross-breeding and subsequent analysis of the characters of the offspring. It is not possible in any case to predict what characters will be found in the offspring of known parents, although in certain instances, to be brought out later, this may be done with some degree of accuracy.

(7) The Effects of Isolation

Most evolutionists believe that a necessary condition for the formation of new species is the isolation, separation, or segregation of certain individuals from others of their kind. This may be due to either geographical or physiological causes.

Geographical Isolation. — "In the case of geographic or topographic isolation the isolated group or groups of individuals are actually in another region or locality from the rest of the species, this being the result of migration, voluntary or involuntary" (250, p. 234). We have shown (p. 284) that normally there is an overproduction of animals, and that dispersal is necessary for the preservation of life. "In regions broken by few barriers, migration and interbreeding being allowed, we find widely distributed species, homogeneous in their character, the members showing individual fluctuation and climatic effects, but remaining uniform in most regards. . . . In regions broken by barriers which isolate groups of individuals we find a great number of related species, though in most cases the same region contains a smaller number of genera or families. . . . Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort" (248).

The fauna of islands show in a striking manner the effects of isolation. Some of these islands, if not of volcanic origin and their animals the descendants of individuals that were driven

there by winds or carried on floating objects, have for a very long time been isolated, and this isolation has so changed the character of these animals that they are now recognized as distinct species. There can be no doubt that the species originated from individuals from the mainland, and that the most important factor in their transmutation has been geographical isolation (274).

Physiological Isolation. — Internal differences may cause physiological isolation, a factor in the origin of species as important probably as geographical isolation. Physiological, or, as it is sometimes called, sexual isolation is caused by "the influence of some variation tending to make difficult or impossible wholly free and miscellaneous mating or breeding inside of a species. This variation may be of purely physiological character or may be a structural one: that is, the hindrance to mating may be one of instinctive feeling, a 'race-feeling' depending on an antipathy to odour, to age, to appearance, etc., or may be a slight modification of the copulatory organs making such mating difficult, or even a modification of the egg or the spermatozoids making fertilization difficult. It is a well-known fact that numerous varieties of domesticated animal species rarely breed together, although quite able to, and provided with full opportunity. On the other hand, animals of different species which in Nature rarely or never breed together may, if kept long in confinement, as in zoological gardens, mate and produce young. In each case there seems to be question of a 'race-feeling'; in the first case a sexual aversion keeping apart individuals of the same species, in the second the breaking down of race-feeling that in Nature has sufficed to prevent hybridizing" (250, p. 245). In many cases, if interbreeding does occur, the hybrid offspring are sterile, *e.g.* the mule produced by a cross between a female horse and a male ass. By physiological isolation, then, groups of individuals are formed within the same region. The result is in every way similar to segregation by geographical barriers.

b. Theories

(1) **Heredity**

THE INHERITANCE OF ACQUIRED CHARACTERS. — Up to the middle of the nineteenth century biologists quite generally believed that acquired characters are inherited. Lamarck in his "Fourth Law of Evolution" says: "All that has been acquired, begun or changed in the structure of individuals in their lifetime, is preserved in reproduction and transmitted to the new individuals which spring from those which have inherited the change." Darwin accounts for many adaptations by the inheritance of acquired characters. Many controversies arise because of misunderstandings as to what really constitutes an acquired character. Parts of a man's body may become changed by use or disuse, *e.g.* the arm of a blacksmith reaches a size above the normal because of constant use. If this characteristic influences the germ cells of the blacksmith, and reappears in his offspring, we have an illustration of the transmission of an acquired character.

Weismann (278) is the foremost opponent of the belief in this theory. He led scientists to examine critically all reported cases, and as a result it was found that no case really shows that a character was not inborn instead of acquired. Mutilations, such as the severing of the tails of sheep, have been practiced for countless generations without affecting the tailed condition of each succeeding generation. Many supposed cases of the inheritance of characters produced in individuals by climatic or other external factors are nothing more than the effects of the external stimuli upon the developing organism. For example, certain snails if reared in small vessels of water develop into small adults, but if the eggs of these dwarfs are allowed to develop and the larvæ to grow to maturity in a large vessel of water, the normal size is regained.

It seems probable that whenever an organism is changed by its environment and the change is transmitted to its offspring,

the germ cells as well as the body cells are affected by the external stimuli, and the body cells have no effect upon the germ cells. The theory is also apparently valueless in explaining inheritance in the Protozoa (p. 79).

THE CONTINUITY OF THE GERM PLASM. — The present widespread belief in the theory of the continuity of the germ plasm is largely due to the efforts of Weismann. We have already illustrated the theory in a general way, by the life history of *Volvox* (p. 98, Fig. 47), and in another place (p. 32) have pointed out that the chromosomes are thought by many to be the bearers of hereditary characters.

According to Weismann, there are "two great categories of living substance — hereditary substance or idioplasm, and 'nutritive substance' or trophoplasm" (278, Vol. I, p. 341). He recognizes the chromatin as the idioplasm, and calls the idioplasm of the germ cells, germ plasm. This germ plasm is "never formed *de novo*, but it grows and increases ceaselessly; it is handed on from one generation to another like a long root creeping through the earth, from which at regular distances shoots grow up and become plants, the individuals of the successive generations" (278, Vol. I, p. 416).

The details of Weismann's theory, and the ingenious explanations of such phenomena as cellular differentiation and regeneration, are extremely complicated. Briefly stated, the mechanism is conceived by Weismann as follows: Each large chromosome of a germ cell is composed of chromatin granules, called "ids." Each id is either male or female, and contains all of the "complexes of primary constituents necessary to the production of a complete individual" (278, p. 349). The production of a particular part of an organism is the rôle of the primary constituents of the id, and, since these determine the nature of the part produced, they are named "determinants." Finally the determinants are composed of one or more particles, called "biophors." These are "far below the limits of visibility," but are "larger than any chemical molecules because they themselves consist of

a group of molecules, among which are some of complex composition, and therefore of relatively considerable size" (278, p. 369).

GALTON'S LAW OF ANCESTRAL INHERITANCE.—Francis Galton, from a study of pedigreed dogs and the genealogical records of the British Peerage, came to the conclusion that in an organism of bisexual parentage, "The two parents between them contribute on the average one half of each inherited faculty, each of them contributing one quarter of it. The four grandparents contribute between them one quarter, or each of them one sixteenth; and so on, the sum of the series $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \ldots$ being equal to 1, as it should be." It has been demonstrated that this law is only an approximation of the real result (241).

MENDEL'S LAW OF INHERITANCE (227).—The results of Mendel's experiments in hybridizing peas and other plants were published by him in 1866, but did not receive any attention from biologists until 1900, when they were discovered in an obscure periodical by several botanists. Since the latter date, Mendel's law has become a favorite object of investigation with both botanists and zoologists, until now its complexities are so great as to make the details of the subject unintelligible except to persons working in this particular field.

An outline of one of Mendel's experiments will serve to illustrate his law (269). The varieties of the edible pea were selected by him for hybridization. When a tall pea was crossed with a dwarf pea, all of the offspring were tall. "Tallness," therefore, is said to be a dominant character (*D*) and "dwarfness" a recessive character (*R*).

When the hybrids were allowed to fertilize themselves, three fourths of their offspring were tall (*D*) and one fourth dwarf (*R*); there were no intermediate forms. When these dwarfs were allowed to fertilize themselves, only dwarf offspring resulted. When the tall peas were allowed to fertilize themselves, one third of them produced tall offspring, which when inbred produced only tall peas; the other two thirds when inbred produced three fourths tall (*D*) and one fourth dwarf (*R*) offspring. The result

may be expressed diagrammatically as in Figure 157 (269). Many other plants and numerous animals have been experimented with; in some cases Mendel's law has been confirmed; in other cases the inheritance is apparently determined in a different way.

To account for the inheritance of characters in the Mendelian ratio of three dominants (*D*) to one recessive (*R*), the theory of the segregation of germ cells has been proposed. This is that the "germ cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types, and consequently incapable of transmitting the opposite character; that when such pure similar gametes of opposite sexes are united in fertilization, the individuals so formed and their posterity are free from all taint of the cross; that there may be in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters" (Bateson).

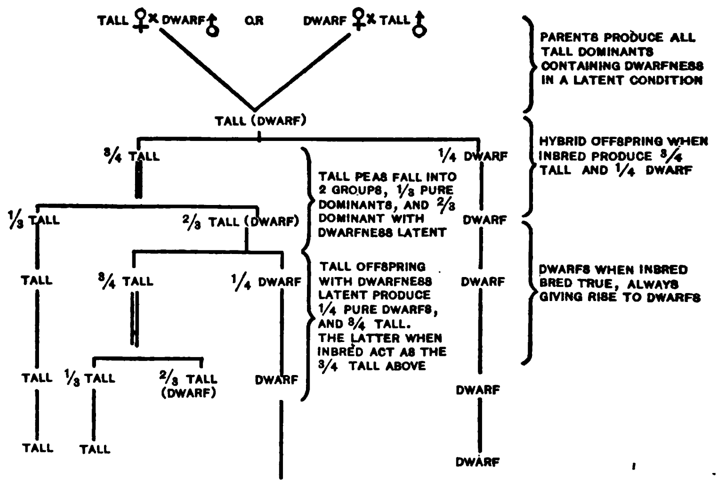


FIG. 157. Diagram showing the inheritance of tallness and dwarfness in peas according to Mendel's Law. (Modified after Thomson.)

(2) Evolution

INTRODUCTION. — In the list of phyla of the animal kingdom on pages 5 to 6, the approximate number of described species belonging to each is given. The sum total of all these is 265,050 of living and 39,905 of fossil forms.[1] The origin of these different species may be accounted for in three ways: (1) by special creation (see p. 8), (2) by spontaneous generation (see p. 8), or (3) by evolution. The first two theories are no longer considered seriously by biologists; some of the evidence for evolution will be found in the following pages. We are not concerned here with the question of the origin of life; but shall try to show that species have evolved from one another or have descended from common ancestors.

THE ARGUMENTS FOR EVOLUTION. — Evidence may be derived from the study of comparative anatomy, embryology, paleontology, and geographical distribution to prove that organic evolution has taken place.

(*a*) *Comparative Anatomy.* — Homologous structures, *i.e.* structures that are anatomically similar, point to a common ancestry for the species possessing them. The fore limbs of the bird, dog, man, and bat (Fig. 158) possess the same fundamental structure, though each is modified for particular functions. Their similarity is explained by the fact that the animals bearing them have all descended from a common ancestor; their dissimilarity by the fact that they are used for different purposes. Vestigial organs, such as the muscles of the ear, and the appendix of man, are structures which are of no use to him now, but were functional in his ancestors. They indicate to us some of the characteristics of these ancestors (256).

(*b*) *Embryology.* — This subject may be dismissed by referring the reader to the discussion of the law of biogenesis on page 228.

[1] This is a very conservative estimate and is undoubtedly a lesser number than have really been described. The number is increasing every year, since new species are being described almost daily.

(*c*) *Paleontology* — The study of fossil animals has brought out some remarkably convincing evidence of organic evolution.

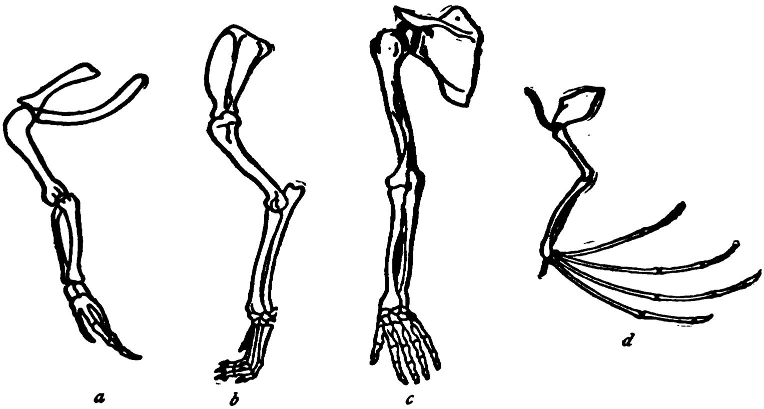


FIG. 158. Skeletons of the fore limbs of various vertebrates. *a*, wing of bird; *b*, fore leg of dog; *c*, arm of man; *d*, wing of bat. (From Metcalf.)

Table XV on page 280 shows that in the oldest strata of the earth's crust containing organic remains, the Cambrian and Silurian, only invertebrates existed. Toward the end of the latter period fishes made their appearance, then amphibians, reptiles, mammals, and finally Man. Each of these groups is of a higher order than the last, and the species in each group become more complex as the present era is approached, a fact not shown in the table.

Even more convincing are the facts revealed by a study of the ancestors of a single species, such as the common horse, *Equus* (Fig. 159). The horses of the Eocene period are represented by *Orohippus*, an animal possessing four-toed fore feet and three-toed hind feet. This form was replaced by *Mesohippus* in the Lower Miocene; then *Protohippus* appears in the Lower Pliocene, *Pliohippus* in the Pliocene, and finally the *Equus* of recent times. In these forms there has been a gradual degeneration of certain

toes, and a corresponding increase in the size of one toe, until an animal, *Equus*, is evolved with one toe on each foot and the splintlike remains of what were functional toes in its Eocene ancestor.

(*d*) *Geographical Distribution.* — The facts of geographical distribution all seem to show that species originate in some particular place, from which they disperse as their numbers increase. When groups are prevented from mingling with others of their kind by environmental barriers or physiological conditions, the factor of isolation, combined with other factors, result in the evolution of new geographical races and finally new species. Accordingly, when species that resemble each other closely are found occupying neighboring regions, but separated by barriers, we conclude that they have evolved from a common ancestor, and have diverged until their differences are considered of specific rank.

The Theory of Natural Selection. — The origin of species, as conceived by Darwin, is largely due to natural selection. We may gain a clear idea of what is meant by natural selection if we examine the results of artificial selection. For example, there are at the present time over one hundred and fifty different domestic varieties of pigeons; a few of these are shown in Figure

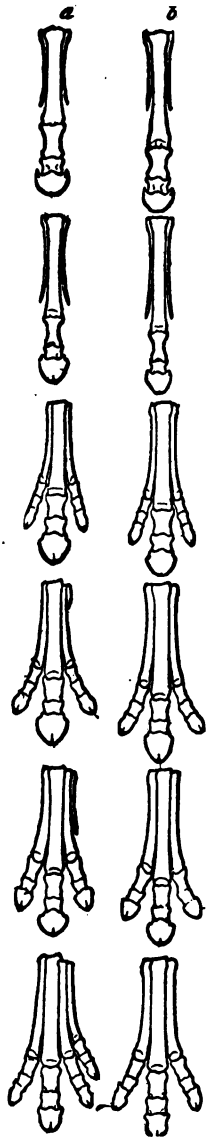


Fig. 159. Diagrams illustrating the gradual changes in foot structure in fossil and recent species of the horse family. *a*, bones of the fore foot; *b*, bones of the hind foot. (From Metcalf after Marsh.)

160. They differ widely from one another in structure and habits, but in many cases may be traced back to a single ancestor, the blue-rock pigeon (*Columba livia*), still in existence in its wild state (Fig. 160, 1). The theory is that these pigeons have been originated by the preservation for breeding purposes of birds that showed favorable variations.

Now animals vary in a wild state as well as under the care of man, and whenever an individual appears with a variation of value in the struggle for existence, this particular animal becomes one of the fittest to survive, and, therefore, lives to transmit its favorable variation to its offspring. In other words, it is selected by nature just as a domesticated animal with a favorable variation is selected by Man. As an example, we may take the robin. We have shown (p. 283) that this bird rears a number of young each year, yet the number of robins remains practically constant from year to year. The majority are killed in some way. Those that are strongest and are able to weather the storms, or are endowed with extreme speed so as to escape their enemies, are selected by Nature, while weaker or slower individuals are doomed to destruction.

Animals become adapted to their surroundings through the operation of this process of natural selection. The wonderfully adapted structures on the legs of the honeybee for gathering pollen may have evolved in this way.

Of recent years many biologists have questioned the adequacy of natural selection to explain all the modifications of species. This was never claimed for the theory, even by Darwin, for he says, in the introduction to the *Origin of Species*, " I am convinced that natural selection has been the main, but not the exclusive, means of modification " (236).

THE THEORY OF ORTHOGENESIS. — Many phenomena of the evolution of organisms cannot be explained by natural selection. For example, the development of structures of apparently no advantage to the animal, such as the arrangement of the veins in the wings of insects, and the development of modifications harmful

FIG. 160. Varieties of domestic pigeons. 1, wild blue-rock pigeon; 2, homing pigeon; 3, common mongrel pigeon; 4, archangel; 5, tumbler; 6, bald-headed tumbler; 7, barb; 8, pouter; 9, Russian trumpeter; 10, fairy swallow; 11, black-winged swallow; 12, fantail; 13, carrier; 14 and 15, bluetts. (From Metcalf.)

to the race and leading to extinction, structures such as paleontologists tell us have appeared many times during the history of the animal kingdom, and illustrated by the Irish stag whose antlers became so enormous as to make it unfit for existence. There appears to be a tendency for modifications to follow certain definite paths, and for certain structures to progress in predetermined directions regardless of their utility, and without the aid of natural selection. This evolution in a definite predetermined direction is known as orthogenesis.

There are a number of theories of orthogenesis. The one most in favor is that which ascribes the control of modifications to the direct effects of physicochemical factors on organisms. Some of the arguments for orthogenesis are derived from the following phenomena: the presence of similar variations in species belonging to one family, the development of disadvantageous structures leading to extinction (*e.g.* the antlers of the Irish stag), the limits of variation due to the chemical composition of the body, the influence of one organ upon another, which limits variation, and the persistence of variations in definite directions so that evolution is not in radiating lines as natural selection demands (264). According to orthogenesis, certain lines of development remain stationary, while others advance.

The theory of orthogenesis in some form or other is accepted by many specialists, working in widely separated fields. Of these may be mentioned Eimer (239, butterflies, birds, and lizards), Whitman (280, pigeons), Tower (270, beetles), and Ruthven (266, snakes). The papers of these men furnish excellent concrete examples of how orthogenesis is supposed to operate.

THE MUTATION THEORY. — A mutant is an organism that differs from its parent in certain well-marked characteristics, which it transmits to its offspring. De Vries is the foremost exponent of the mutation theory, and it is his work that has given it world-wide recognition. The conclusions of de Vries are based on a study of the evening primrose (*Œnothera lamarckiana*). The mutation theory may be stated in his words as follows: "The way in which

one species originates from another has not been adequately explained. The current belief assumes that species are slowly changed into new types. In contradiction to this conception the theory of mutation assumes that new species and varieties are produced from existing forms by sudden leaps. These may arise simultaneously and in groups, or separately at more or less widely distributed periods" (272).

While directly opposed to Darwin's theory of the origin of species in regard to the kinds of variations selected, de Vries gives Darwin credit for the discovery of the "great principle which rules the evolution of organisms. It is the principle of natural selection. It is the sifting out of all organisms of minor worth through the struggle for life. It is only a sieve, and not a force of nature, no direct cause of improvement, as many of Darwin's adversaries, and unfortunately many of his followers also, have so often asserted. It is only a sieve, which decides which is to live, and what is to die. . . . By this means natural selection is the one directing cause of the broad lines of evolution" (272, p. 6). De Vries claims, however, that "species and varieties have originated by mutation, and are, at present, not known to originate in another way."

Two sorts of species are recognized by de Vries, the systematic species of the systematist, and elementary species, which are more numerous and are described as "any form which remains constant and distinct from its allies" (272, p. 10). Elementary species have unit characters which are indivisible and distinct in inheritance. All organisms are not mutable to the same degree, and to observe the origin of species, "It is only necessary to have a plant in a mutable condition" (272, p. 26).

Since the publication of de Vries' results biologists have examined the data from a large number of experiments, but only a comparatively small amount of proof is available to support the theory from the zoological side.

Perhaps the best attitude to take toward the three theories outlined in the last few pages is that of Professor Whitman, who

says, "natural selection, orthogenesis, and mutation appear to present fundamental contradictions; but I believe that each stands for truth, and reconciliation is not distant" (280).

2. The Social Life of Animals

Very few animals lead a solitary life, and even those that may be considered solitary are influenced indirectly by others, just as cats, by destroying field mice, determine the number of bumblebees in a given locality (see p. 262). The various grades of partnership and cooperation are recognized by the terms *commensalism*, *symbiosis*, *parasitism*, and *social life.*

a. Commensalism

This is a term used to indicate a loose association of two kinds of organisms from which one may derive benefit at the expense of the other. In some cases one species eats at the table of another without contributing anything in return. The guest bumblebee, that frequents the nests of the true bumblebees and lives upon the food stored there, belongs to this class. The barnacles which attach themselves to the skin of whales derive benefit from being carried about, and, although they do not seriously inconvenience their bearer, they fail to pay their fare.

b. Symbiosis

In symbiosis the association between the two kinds of organisms is intimate and persistent, often showing marked cooperation and being mutually advantageous. This kind of partnership may have had its origin in the more simple commensalism, or may have arisen from parasitism. Several illustrations of symbiotic relations have already been discussed in this book, that between two plants (the lichen, p. 143), that between a plant and an animal (*Hydra* and the green alga, *Zoochlorella*, p. 143), and that between two animals (the hermit crab and a Cœlenterate, p. 143).

One more illustration may be cited to show how remarkable the relations between certain plants and animals may become. The flowers of the genus *Yucca* depend upon a single species of insect, the Pronuba moth, for their cross-pollination. This little white moth visits the flowers in the evening. It scrapes some pollen from a stamen, holds it underneath its head, and carries it to another flower. It clings to the pistil of this, and, thrusting its ovipositor through the wall of the ovary, lays an egg. It then mounts the pistil, and forces the pollen it has brought down into the stigmatic tube. Another egg is laid in another part of the ovary, and more pollen is inserted into the stigmatic tube. These processes may be repeated half a dozen times in a single flower. The advantage to the flower is, of course, the certainty of being cross-pollinated and of producing seeds. These seeds provide a supply of food for the larvæ that hatch from the eggs laid by the moth in the ovary. The seeds are so numerous that the few eaten by the larvæ may well be spared (267).

c. *Parasitism*

A parasitic animal is one that lives upon another organism. This is also a definition of a predaceous animal. We may distinguish between the two, however, by assuming that parasites are always carried on or in the bodies of their victims, whereas predaceous animals are free-living. The fleas are common examples of external parasites. The malaria parasite (p. 88, Fig. 42) and the round worm (p. 160, Fig. 81) are internal parasites. The life histories of these species, as given on the pages referred to, will suffice to illustrate parasitic habits, but certain characteristics resulting from this kind of life will be pointed out briefly.

Parasites as a rule are comparatively simple in structure. This is due to degeneration and not to a low position in the animal kingdom. In many cases the reproductive organs are exceedingly well-developed, whereas organs of locomotion, digestion, etc., become almost functionless.

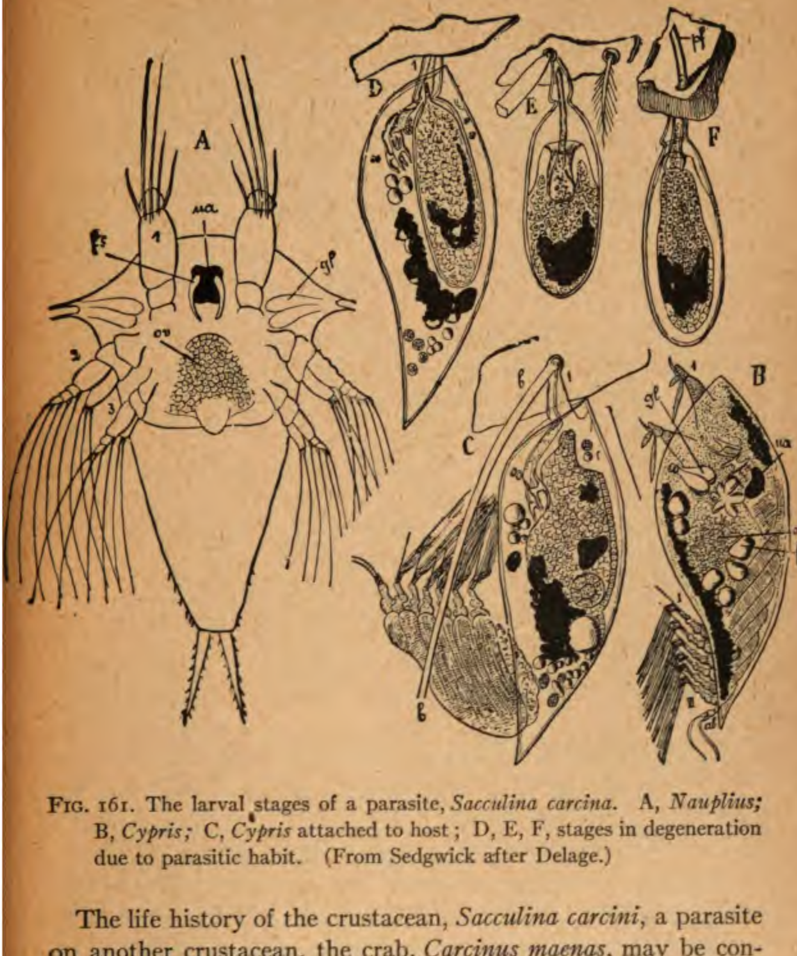


FIG. 161. The larval stages of a parasite, *Sacculina carcina*. A, *Nauplius;* B, *Cypris;* C, *Cypris* attached to host; D, E, F, stages in degeneration due to parasitic habit. (From Sedgwick after Delage.)

The life history of the crustacean, *Sacculina carcini*, a parasite on another crustacean, the crab, *Carcinus maenas*, may be considered a good illustration of the degeneration of parasites. *Sacculina* hatches as a *Nauplius* (Fig. 161, A), which soon changes to the *Cypris* stage (B). After swimming about for two or three days, the larva attaches itself to the setæ of a crab by means of its antennæ (*1*). The base of the seta is penetrated by the hollow

antenna, and the larval *Sacculina* sheds its appendages, shell, muscles, and excretory organs. What remains (E) passes through the antenna into the body of the crab (F), and finally reaches the body cavity. A system of roots now grows out in all directions. When the crab molts, the saclike body of the parasite penetrates to the outside, resembling a tumor consisting almost entirely of reproductive organs (237).

(*d*) *Social Life*

That there is a continual competition among individuals and species has been pointed out in the course of our discussion of geographical distribution (p. 275), and the struggle for existence (p. 283). However, there is another law of nature, namely sociability, not so far-reaching, perhaps, but of undoubted importance to the welfare of many and diverse species of animals. Certain of the social species have already been mentioned (p. 264), and the activities of the honeybee, an insect with a very complex social life, have been described in some detail (p. 233).

The beavers, Rocky Mountain sheep, and prairie dogs (mammals), the swallows, herons, and sea gulls (birds), and the ants, wasps, and termites (insects) are famous for their community life.

The advantages of living together are many, and the lives of most of the gregarious animals depend upon their instinct to form bands and colonies. Darwin recognized the value of social life, although his theories were based largely upon the effects of the struggle for existence. He says that "the individuals which took the greatest pleasure in society would best escape various dangers; while those that cared least for their comrades, and lived solitary, would perish in greater numbers." Deer, for example, when banded together may escape from their enemies, whereas single individuals would be destroyed. The Rocky Mountain sheep post sentinels, which warn the main herd of the approach of danger, and enable all to seek places of safety.

The gregarious habit is also of value for offense, as in the case of wolves that hunt in packs, and not infrequently the weak band together and attack the strong, for example, the swallows that unite to drive away birds of prey. Combined activities of other kinds also occur; certain beetles help one another to bury small dead animals in which their eggs are laid; the monarch butterflies, as well as most of the birds, congregate in the autumn, and migrate southward together.

The steps in the progress toward a social life are extremely interesting (268).

(1) In the lowest animals, the Protozoa, there are certain species, like *Volvox* (Fig. 46, p. 97), that consist of colonies of cells resembling the early stages in the development of a Metazoon (see p. 107).

(2) Some of the many-celled animals of almost every phylum form colonies, which contain individuals physically different because of their functions, but all referable to a common type and all mutually dependent; for example, the Portuguese man-of-war among the Cœlenterates (Fig. 67, p. 142).

(3) The love of mates constitutes a third step in social progress. Many of the higher Metazoa, such as insects and fish, but especially birds and mammals, mate and become mutually helpful.

(4) The love of mates leads to family life, as exemplified by ants, bees, birds, beavers, and many other animals.

(5) And finally society, which is the combination of families, represents the most advanced stage of social life.

In conclusion we may say with Kropotkin, "While fully admitting that force, swiftness, protective colors, cunning, and endurance of hunger and cold, which are mentioned by Darwin and Wallace as so many qualities making the individuals or the species the fittest under certain circumstances, we maintain that under *any* circumstances sociability is the greatest advantage in the struggle for life. . . . The fittest are thus the most sociable animals, and sociability appears as the chief factor of evo-

lution, both directly, by securing the well-being of the species while diminishing the waste of energy, and indirectly by favoring the growth of intelligence. . . . Therefore combine — practice mutual aid. That is the surest means of giving to each and to all the greatest safety, the best guarantee of existence and progress — bodily, intellectual, and moral. That is what nature teaches us."

3. Reflexes, Instincts, and the Animal Mind

a. Reflexes

In the Metazoa the reflex, carried on either consciously or unconsciously, is considered the physiological unit of nervous activity. It requires in its simplest form a sensory neuron, the receptor, a motor neuron, the adjustor, and the organ stimulated to activity, the effector (see p. 179). The stimulus passes from the receptor to the adjustor and is reflected to the effector. This apparent reflection suggested the term "reflex."

The reflex, according to the above idea, is operative only in the case of animals with nervous systems. If we would include certain lower Metazoa and the Protozoa, our definition must be changed so as to take into account the action, and not the mechanism that is responsible for the action. According to this view, any simple response to a stimulus is a *reflex*. The avoiding reaction of *Paramecium* (Fig. 33, p. 74) is known as a reflex, and the activities of *Paramecia* and many other lower organisms are supposed by some to be a series of reflexes to external stimuli. But if examined carefully, the reactions of lower organisms are not as simple as they at first appear. For example, the avoiding reaction of *Paramecium* is not always exactly the same. "If the animal be taken as a center about which a sphere is described, with a radius several times the length of the body, then as a result of the avoiding reaction the animal may traverse the peripheral surface of this sphere at *any point*, moving at the time either backward or forward. *Paramecium*, in spite of its curious limi-

tations as to method of movement, is as free to vary its relations to the environment in response to a stimulus as an organism of its form and structure could conceivably be. Such behavior does not fall within the concept of a reflex if the latter is defined as a uniform reaction" (246, p. 279). Jennings has pointed out that before the reflex can be considered a simple invariable unit for behavior, the physiological condition of the organism must be taken into account. Such a unit might be illustrated as follows: stimulus A, acting upon an animal whose physiological state is B, gives reaction C.

b. *Instinct*

Instinct is "the faculty of acting in such a way as to produce certain ends, without foresight of the ends, and without previous education in the performance" (James). Instinctive acts are all complex. They are performed in a similar manner by all members of the same sex and race. Those of the social animals are remarkably varied. Our study of the honeybee (Chap. XII) has given us sufficient knowledge of this insect to warrant our using it to illustrate certain kinds of instincts.

The queen's nuptial flight and her copulation with the drone is instinctive. She acts without previous experience, and accomplishes the filling of her spermatheca with spermatozoa without apparently realizing the purpose of the whole performance. The selection of a hollow tree by worker scouts, and the cleaning of it in preparation for the swarm, is instinctive. The many activities that follow the advent into a new home, such as crevice chinking, varnishing, wax forming, comb building, egg laying, gathering and storing pollen and nectar, ripening honey, guarding, cleaning, and ventilating the hive, and caring for the queen and young bees, are the results of instincts.

The instinct of caring for the young is of special interest, since those animals that care for their young succeed in rearing a larger proportion than those that allow their offspring to shift for them-

selves. The division of labor among the workers is due to instinct; although each individual is equipped with the many structural features that so wonderfully adapt it to its mode of life, only one sort of work is undertaken at a time, and this in all cases is the thing most needed by the hive. For example, as soon as a hollow tree is selected and cleaned, the workers proceed to secrete wax and build comb; when eggs are laid, pollen is gathered and stored with which to feed the forthcoming larvæ; during the pollen and nectar gathering season, each worker collects either the one or the other, and the pollen gathered on one trip is all of one color, having been collected evidently from one kind of flower. Altruistic instincts such as these are especially abundant in social animals, and among these may be classed the social instinct itself. On the other hand, the instincts of feeding, of self-defense, of battling for the supremacy of the hive, and of playing before the hive on bright days, may be said to be egoistic.

These definitions and examples of instinctive acts are not accepted by all scientists; and of recent years there has been a tendency to consider them as tropic responses to stimuli. Thus one authority attributes all the activities of ants and bees to reflex responses to chemical and other stimuli (229). The eminent physiologist Loeb says: "My investigations on the heliotropism of animals led me to analyze in a few cases the conditions which determine the apparently accidental direction of animal movements which, according to traditional notions, are called voluntary or instinctive. Wherever I have thus far investigated the cause of such 'voluntary' or 'instinctive' movements in animals, I have without exception discovered such circumstances at work as are known in inanimate nature as determinate movements. By the help of these causes it is possible to control the 'voluntary' movements of a living animal just as securely and unequivocally as the engineer has been able to control the movements in inanimate nature. What has been taken for the effect of 'will' or 'instinct' is in reality the effect of light, of gravity, of friction, of chemical forces, etc." (252, p. 107). According

to this author, " For the inheritance of instincts it is only necessary that the egg contain certain substances — which will determine the different tropisms — and the conditions for producing bilateral symmetry of the embryo " (251).

Many other competent authorities maintain that " we cannot exclude a psychic element from the definition of ' instinct ' without ignoring its very nature and taking it for a reflex motion, . . . " (277, p. 9), and that in both the lower and higher animals " the behavior is not as a rule on the tropism plan — a set, forced method of reacting to each particular agent — but takes place in a much more flexible, less directly machinelike way, by the method of trial and error . . . " although " tropic action doubtless occurs . . ." (245, p. 252).

c. The Animal Mind

Mind is " The individual's conscious process, together with the dispositions and predispositions which condition it. It is thus the individual's consciousness, with its capabilities; its capabilities including all faculties, powers, capacities, aptitudes, and dispositions, acquired and innate " (226, Vol. II, p. 82). We may hope to determine, therefore, the character of an animal's mind by attempting to investigate its conscious behavior.

We should understand at the beginning of cur discussion that there is no general agreement with regard to the presence of mind in animals. One school of investigators believes that all animals are conscious; another, that only those that show certain kinds of behavior should be considered conscious; and a third school holds that there is no evidence of mind, and that comparative psychology should be abandoned, and behavior should be explained in physiological terms. Certain members of these schools believe with Forel that it is " possible to demonstrate the existence of memory, associations of sensory images, perceptions, attention, habits, simple powers of inference from analogy, the utilization of individual experience, and hence distinct, though feeble,

plastic individual deliberations or adaptations" (240, p. 36). Other authorities consider the power to learn by individual experience, for example, the habit-forming in the crayfish (p. 223), as evidence of mind. And still others deny the presence of mind, attributing every act to chemicophysical processes.

It certainly is true that no one knows whether animals are conscious or not. Our evidence is all gained by inferences from behavior. The conditions under which the facts of behavior are obtained are of great importance. Anecdotes are of little value, since the observer is not scientifically trained, and, wishing to tell a good story, tends to exaggerate the apparent intelligence of the animal. The modern method is that of carrying out definite experiments, the habits of the species and past experiences of the individuals being known. The conclusion is then based on the least complex interpretation that will account for the facts of behavior observed. We can, however, only interpret behavior on the analogy of human experience, the tendency being to ascribe human traits to animals.

Learning by experience, a process considered by many indicative of intelligence, is one of the criteria of the presence of mind; but the modifiability of the behavior must be rapid, or time enough for a change in body structure may elapse. Structure is a distinct help in inferring mind, since animals with a nervous system similar to that of Man must be affected by external stimuli in a similar way.

"We know not where consciousness begins in the animal world. We know where it surely resides — in ourselves; we know where it exists beyond a reasonable doubt — in those animals of structure resembling ours which rapidly adapt themselves to the lessons of experience. Beyond this point, for all we know, it may exist in simpler and simpler forms until we reach the very lowest of living beings" (276, p. 36).

BIBLIOGRAPHY

A few of the books and articles that have been consulted in preparing this work will be found in the following list. They have been selected chiefly with reference to their accessibility and value to students, and are arranged alphabetically under the headings of the various chapters. Their numbers, corresponding to numbers in parentheses in the text, will facilitate the finding of any particular source of information.

CHAPTER I

INTRODUCTION

1. **Aspects of the Species Question.** — Papers read at a symposium at Chicago, Jan. 1, 1908. 1908. Amer. Nat., vol. 42, pp. 218–281.
2. **Darwin, C.**, 1861. — The Origin of Species by means of Natural Selection. New York.
3. **Harmer, S. F., and A. E. Shipley.** — Editors. The Cambridge Natural History. 10 vols. London.
4. **Lertwig, R.**, 1902. — Manual of Zoology. Translated by J. S. Kingsley. New York.
5. **Lankester, E. R.** — Editor. A Treatise on Zoology. London.
6. **Parker, G. H.** 1908. — Zoological Progress. Amer. Nat., vol. 42, pp. 115–133.
7. **Parker, T. J., and W. A. Haswell**, 1897. — Text-book of Zoology. 2 vols. London.
8. **Thomson, J. A.**, 1906. — Outlines of Zoology. 4th ed. London.
9. **Williston, S. W.**, 1908. — What is a Species? Amer. Nat., vol. 42, pp. 184–194.
10. **Zittel, K. A. von**, 1900–1902. — Text-book of Palæontology. 2 vols. Translated by C. R. Eastman. London.

CHAPTER II

PHENOMENA OF LIFE

11. **Bütschli, O.**, 1894. — Investigations on Microscopic Foams and on Protoplasm. London.
12. **Dahlgren, U., and W. A. Kepner**, 1908. — Text-book of the Principles of Animal Histology. New York.

13. **Lee, F. S.**, 1908. — Physiology. Amer. Nat., vol. 42, pp. 394–417.
14. **Locy, W. A.**, 1908. — Biology and its Makers. New York.
15. **Loeb, J.**, 1906. — The Dynamics of Living Matter. New York.
16. **Sedgwick, W. T., and E. B. Wilson**, 1899. — General Biology. 2d ed. New York.
17. **Verworm, M.**, 1899. — General Physiology. Translated by F. E. Lee. London.
18. **Wilson, E. B.**, 1899. — On Protoplasmic Structure in the Eggs of Echinoderms and Some Other Animals, Journ. of Morph., vol. 15, Suppl., pp. 1–28.
19. ——, 1900. — The Cell in Development and Inheritance. 2d ed. New York.
20. ——, 1908. — Biology. New York.

CHAPTER III

THE CELL AND THE CELL THEORY

21. **Dahlgren, U., and W. A. Kepner**, 1908. — Text-book of the Principles of Animal Histology. New York.
22. **Farmer, J. B.**, 1903. — The Structure of Animal and Vegetable Cells. In Lankester's Treatise on Zoology, Part I, 2d fascicle. London.
23. **Hertwig, O.**, 1895. The Cell. Translated by M. Campbell and edited by H. J. Campbell. London.
24. **Locy, W. A.**, 1908. — Biology and its Makers. New York.
25. **Wilson, E. B.**, 1900. — The Cell in Development and Inheritance. 2d ed. New York.

CHAPTER IV

AMEBA

26. **Bernstein, J.**, 1900. — Chemotropische Bewegungen eines Quecksilbertropfens. Arch. f. d. ges. Physiol., Bd. 80, pp. 628–637.
27. **Berthold, G.**, 1886. — Studien über Protoplasmamechanik. Leipzig.
28. **Bütschli, O.**, 1894. — Investigations on Microscopic Foams and on Protoplasm. London.
29. **Calkins, G. N.**, 1901. — The Protozoa. New York.
30. ——, 1905. — Evidences of a Sexual cycle in the Life-History of Amœba proteus. Archiv f. Protist., vol. 5, pp. 1–16.
31. ——, 1907. — The Fertilization of Ameba proteus. Biol. Bull., vol. 13, pp. 219–230.

32. ——, 1909. — Protozoology. Philad.
33. **Davenport**, C. B., 1897. — Experimental Morphology, vol. I. New York.
34. **Dellinger, O. P.**, 1906. — Locomotion of Amœbæ and Allied Forms. Journ. of Exp. Zool., vol. 3, pp. 337–358.
35. **Harrington and Leaming**, 1900. — The Reaction of Amœba to Light of Different Colors. Amer. Journ. Physiol., vol. 3, pp. 9–18.
36. **Hofer**, B., 1889. — Experimentelle Untersuchungen über den Einfluss des Kerns auf das Protoplasma. Jenaische Zeitschrift, Bd. 17, 105–176.
37. **Jennings**, H. S. — Methods of Cultivating Amœba and Other Protozoa for Class Use. Journ. Appl. Micros. and Lab. Methods, vol. 6, p. 2406.
38. ——, — A Method of Demonstrating the External Discharge of the Contractile Vacuole. Zool. Anz., Bd. 27, pp. 656–658.
39. ——, 1904. — Contributions to the Study of the Behavior of Lower Organisms. Carnegie Institution of Washington.
40. ——, 1904. — Physical Imitations of the Activities of Amœba. Amer. Nat., vol. 38, pp. 625–642.
41. ——, 1906. — Behavior of the Lower Organisms. New York.
42. **Kuhne**, W., 1864. — Untersuchungen über das Protoplasma und die Contractilität. Leipzig.
43. **Leidy**, J., 1879. — Freshwater Rhizopods of North America. Report of the U. S. Geol. Survey of the Territories, vol. 12.
44. **Rhumbler**, L., 1898. — Physikalische Analyse von Lebenserscheinungen der Zelle. Arch. f. Entw.-mech., Bd. 7, pp. 103–350.
45. **Schaudinn**, F., 1895. — Über die Theilung von Amœba binucleata Gruber. Sitz. Ber. Ges. Nat. Freunde Berlin, pp. 130–141.
46. **Sheel**, C., 1899. — Beiträge zur Fortpflanzung der Amöben. Fests z. Siebenzigsten Geburtstag von C. V. Kupffer, pp. 569–580.
47. **Schulze**, F. E., 1875. — Rhizopodenstudien. Arch. f. Mikr. Anat., Bd. 11, pp. 329–353.
48. **Verworm**, M., 1899. — General Physiology. Translated by F. E. Lee. London.

CHAPTER V

PARAMECIUM

49. **Benda**, C., 1901. — Ueber neue Darstellungsmethoden, etc. Arch. f. Anat. u. Physiol., Suppl., Pts. 1–2, pp. 147–157.
50. **Boubier**, A.M., 1907. — La vesicule contractile, organe hydrostatique. Ann. Biol. lacustre, Bruxelles, t. 2, pp. 214–219.

51. **Brooks, W. K.**, 1904. — The Foundations of Zoology. New York.

52. **Calkins, G. N.**, 1901. — The Protozoa. New York.

53. ——, 1909. — Protozoology. Philad.

54. —— and **S. W. Cull**, 1907. — The Conjugation of Paramecium aurelia (caudatum). Archiv. f. Protist., vol. 10, pp. 375–415.

55. **Cull, S. A.**, 1907. — Rejuvenescence as the Result of Conjugation. Journ. Exp. Zool., vol. 4, pp. 85–89.

56. **Dellinger, O. P.**, 1909. — The Cilium as a Key to the Structure of Contractile Protoplasm. Journ. Morph., vol. 20, pp. 171–210.

57. **Hamburger, C.**, 1904. — Die Conjugation von Paramecium bursaria Focke. Archiv. f. Protist., vol. 4, pp. 199–239.

58. **Hertel, E.**, 1904. — Ueber Beeinflussung des Organismus durch Licht, etc. Zeitsch. f. allg. Physiol., Bd. 4, pp. 1–43.

59. **Jennings, H. S.**, 1901. — On the Significance of the Spiral Swimming of Organisms. Amer. Nat., vol. 35, pp. 369–378.

60. ——, 1904. — A Method of Demonstrating the External Discharge of the Contractile Vacuole. Zool. Anz., Bd. 27, pp. 656–658.

61. ——, 1904. — Contributions to the Study of the Behavior of Lower Organisms. Carnegie Institution of Washington.

62. ——, 1906. — Behavior of the Lower Organisms. New York.

63. ——, 1908. — Animal Behavior. Amer. Nat., vol. 42, pp. 754–760.

64. ——, 1908. — The Interpretation of the Behavior of the Lower Organisms. Science., N. S., vol. 27, pp. 698–710.

65. ——, 1909. — Heredity and Variation in the Simplest Organisms. Amer. Nat., vol. 43, pp. 321–337.

66. ——, **and C. Jamieson**, 1902. — The Movements and Reactions of Pieces of Infusoria. Biol. Bull., vol. 3, pp. 225–234.

67. **Jenson, P.**, 1893. — Ueber den Geotropismus niederer Organismen. Arch. f. d. ges. Physiol., Bd. 53, pp. 428–480.

68. **Lyon, E. P.**, 1905. — On the Theory of Geotropism in Paramœcium. Amer. Journ. Physiol., vol. 14, pp. 421–432.

69. **Maier, H. N.**, 1903. — Ueber den feineren Bau der Wimperapparate der Infusorien. Arch. f. Protist., Bd. 2, pp. 73–179.

70. **Mast, S. O.**, 1909. — The Reactions of Didinium nasutum (Stein), with special reference to the Feeding Habits and the Function of Trichocysts. Biol. Bull., vol. 16, pp. 91–118.

71. **Maupas, E.**, 1888. — Recherches Expérimentales sur las Multiplication des Infusiores cilies. Arch. d. Zool. expér. et gén., 2me ser, t. 6.

72. **Mitrophanow, P.**, 1905. — Étude sur la structure, le developpement et l'exposition des trichocystes des Paramecies. Arch. f. Protist., Bd. 5, pp. 78–91.

73. **Schaefer, E.**, 1904. — Theories of Ciliary Movement. Anat. Anz., Bd. 24, pp. 497–511.
74. **Schuberg, A.**, 1905. — Ueber Cilien und Trichocysten einiger Infusorien. Arch. f. Protist., Bd. 6, pp. 61–110.
75. **Williams, L. W.**, 1907. — The Structure of Cilia, especially in Gastropods. Amer. Nat., vol. 41, pp. 545–551.

CHAPTER VI

OTHER PROTOZOA

76. **Blackman, F. F.**, 1900. — The Primitive Algæ and the Flagellata. Ann. Bot., vol. 14, pp. 647–688.
77. **Bourne, G. C.**, 1909. — Comparative Anatomy of Animals., vol. 1, 2d ed. London.
78. **Calkins, G. N.**, 1909. — Protozoology. Philad.
79. **Howard, L. O.**, 1900. — Notes on the Mosquitoes of the United States. Bull. 25, New Series, U. S. Dept. Agric. Div. of Entomology.
80. **Jennings, H. S.**, 1906. — The Behavior of Lower Organisms. New York.
81. **Kent, W. S.**, 1881. — Manual of the Infusoria. London.
82. **Keuten, J.**, 1895. — Die Kerntheilung von Euglena viridis. Zeit. f. wiss. Zool., Bd. 60, pp. 215–235.
83. **Lang, A.**, 1901. — Lehrbuch der Vergleichenden Anatomie der Wirbellosen Thiere, Bd. 1, 2d pt.
84. **Minchin, E. A.**, 1903. — In Lankester's Treatise on Zoology, pt. 1, 2d fascicle.
85. **Oltmanns, F.**, 1904. — Morphologie und Biologie der Algen, Bd. 1. Jena.
86. **Weismann, A.**, 1904. — The Evolution Theory. London. Translated by J. A. Thomson.

CHAPTER VII

INTRODUCTION TO THE METAZOA

87. **Boveri, T.**, 1892. — Die Entstehung des Gegensatzes zwischen den Geschlechtszellen und den somatischen Zellen bei Ascaris megalocephala. Sitz. ges. f. Morph. Physiol. München, Bd. 8.
88. **Calkins, G. N., and S. Cull**, 1907. — The Conjugation of Paramæcium aurelia (caudatum). Archiv. f. Protist., Bd. 10, pp. 375–415.

89. **Dahlgren, U., and W. A. Kepner**, 1908. — Principles of Animal Histology. New York.
90. **Haecker, V.**, 1897. — Die Keimbahn von Cyclops. Arch. Mikr. Anat., Bd. 49, pp. 35–91.
91. **Hatschek, B.**, 1886. — Zur Entwicklung des Amphioxis. Berlin.
92. **Hegner, R. W.**, 1909. — The Origin and Early Development of the Germ-Cells in Some Chrysomelid Beetles. Journ. Morph., vol. 20, pp. 231–296.
93. **Hertwig, R.**, 1897. — General Principles of Zoology. Translated by G. W. Field. New York.
94. **Korschelt, E., and K. Heider**, 1895–1900. — Text-book of the Embryology of Invertebrates. 4 vols. Translated by E. L. Mark and others. London.
95. **Martin, H. N.**, 1894. — The Human Body. 6th ed. New York.
96. **Montgomery, T. H.**, 1901. — A Study of the Chromosomes of the Germ-Cells of the Metazoa. Trans. Amer. Phil. Soc., vol. 20.
97. **Stöhr, P.**, 1898. — Text-book of Histology. Philad.
98. **Weismann, A.**, 1904. — The Evolution Theory. Translated by J. A. Thomson. London.
99. **Wilson, E. B.**, 1900. — The Cell in Development and Inheritance. New York.
100. ——., 1905–1909. — Studies on Chromosomes. Journ. of Exp. Zool., vols. 2–6.

CHAPTER VIII

HYDRA AND CŒLENTERATES IN GENERAL

101. **Bourne, G. C.**, 1909. — Comparative Anatomy of Animals, vol. 1, 2d ed. London.
102. **Brauer, A.**, 1891. — Ueber die Entwicklung von Hydra. Zeit. f. wiss. Zool., Bd. 52, pp. 169–216.
103. **Cambridge Natural History**, 1906, vol. 1.
104. **Downing, E. R.**, 1902. — Ingestion and Digestion in Hydra, Science. N. S. vol. 15, p. 523.
105. ——, 1905. — The Spermatogenesis of Hydra. Zool. Jahrb., Bd. 21, pp. 379–415.
106. ——, 1908. — The Ovogenesis of Hydra fusca. A preliminary paper. Biol. Bull., vol. 15, pp. 63–66.
107. **Frischholz, E.**, 1909. — Zur Biologie von Hydra. Biol. Centralbl. Bd. 29, pp. 182–290.
108. **Glaser, O. C., and C. M. Sparrow**, 1909. — The Physiology of Nematocysts. Journ. Exp. Zool., vol. 6, pp. 361–382.

109. **Hadzi, J.**, 1909. — Ueber das Nervensystem von Hydra. Arbeit. Zool. Inst., Wien, t. 17, pp. 225–268.
110. **Jennings, H. S.**, 1906. — The Behavior of the Lower Organisms. New York.
111. **Koelitz, W.**, 1908. — Fortpflanzung durch Querteilung bei Hydra. Zool. Anz., Bd. 33, pp. 529–536.
112. ——, 1909. — Ueber Längsteilung und Doppelbildungen bei Hydra. Zool. Anz., Bd. 35, pp. 36–46.
113. **Mast, S. O.**, 1903. — Reactions to Temperature Changes in Spirillum, Hydra, and Fresh-Water Planarians. Amer. Journ. Physiol., vol. 10, pp. 165–190.
114. **Parker, T. J., and W. A. Haswell.**, 1897. — Text-book of Zoology. London.
115. **Pearl, R.**, 1901. — Studies on the Effects of Electricity on Organisms, II. The Reactions of Hydra to the Constant Current. Amer. Journ. Physiol., vol. 5, pp. 301–320.
116. **Reese, A. M.**, 1909. — Variations in the Tentacles of Hydra. Science, N. S., vol. 29, p. 433.
117. **Shipley, A. E., and E. W. MacBride**, 1904. — Zoology. Cambridge.
118. **Tannreuther, G. W.**, 1908.— The Development of Hydra. Biol. Bull., vol. 14, pp. 261–280.
119. —— 1909. — Observations on the Germ-Cells of Hydra. Biol. Bull., vol. 16, pp. 205–209.
120. —— 1909. — Budding in Hydra. Biol. Bull., vol. 16, pp. 210–214.
121. **Toppe, O.** — Ueber die Wirkungsweise der Nesselkapseln von Hydra. Zool. Anz., Bd. 33, pp. 798–805.
122. **Trembley, A.**, 1744. — Mémoires pour servir à l'Histoire d'un genre de Polypes d'eau douce à Bras en forme de cornes. Paris.
123. **Wagner, G.**, 1904. — On Some Movements and Reactions of Hydra. Quart. Journ. Micro. Sc., vol. 48, pp. 585–622.
124. **Wilson, E. B.**, 1891. — The Heliotropism of Hydra. Amer. Nat., vol. 25, pp. 413–433.

CHAPTER IX

SPONGES, FLAT WORMS, AND ROUND WORMS

125. **Arnold, A.**, 1909. — Intracellular and general digestive processes in Planariæ. Quart. Journ. Micro. Sc., vol. 54, pp. 207–220.
126. **Bourne, G. C.**, 1908. — Comparative Anatomy of Animals, vol. 2. London.
127. **Cambridge Natural History.** — Vol. 1, 1906, vol. 2, 1896. London.

128. **Drew, G. A.**, 1907. — Invertebrate Zoology. Philadelphia.
129. **Morgan, T. H.**, 1901. — Regeneration. New York.
130. **Parker, G. H.**, 1909. — The Origin of the Nervous System and its Appropriation of Effectors. Pop. Sc. Monthly, vol. 75, pp. 56–64; 137–146; 253–263; 338–345.
131. **Parker, T. J., and W. A. Haswell**, 1897. — Text-book of Zoology, vol. 1. London.
132. **Pratt, H. S.**, 1902. Invertebrate Zoology. Boston.
133. **Shipley, A. E., and E. W. MacBride**, 1904. — Zoology. Cambridge.
134. **Treatise on Zoology**, ed. by E. R. Lankester. Vol. 2, 1900, vol. 4, 1901. London.

CHAPTER X

THE EARTHWORM AND ANNELIDS IN GENERAL

135. **Adams, G. P.**, 1903. — On the Negative and Positive Phototropism of the Earthworm, Allolobophora fœtida, as Determined by Light of Different Intensities. Am. Journ. Physiol., vol. 9, pp. 26–34.
136. **Barker**, 1907. — The Neuron Theory. Review of Harvey Lectures for 1905–1906. Science, N. S., vol. 26, p. 633.
137. **Bourne, G. C.**, 1908. — Comparative Anatomy of Animals, vol. 2. London.
138. **Bugnion, E, and N. Popoff**, 1905. — La spermatogénèse du Lombric terrestre. Arch. Z. Expér. (4), t. 3, pp. 339–389.
139. **Darwin, C. R.**, 1883. — The Formation of Vegetable-Mould through the Action of Worms, with Observations on their Habits. New York.
140. **Depdolla, P.**, 1905. — Untersuchungen über die Spermatogenese von Lumbricus terrestris. Zool. Anz., Bd. 28, pp. 545–557.
141. **Foot, K.**, 1898. — The Cocoons and Eggs of Allolobophora fœtida. Journ. Morph., vol. 14, pp. 481–506.
142. ——, **and E. C. Strobell**, 1902. — Further Notes on the Cocoons of Allolobophora fœtida. Biol. Bull., vol. 3, pp. 206–213.
143. **Harrington, N. S.**, 1899. — The Calciferous Glands of the Earthworm with Appendix on the Circulation. Journ. Morph., Supp., vol. 15, pp. 105–168.
144. **Hesse, R.**, 1896. — Untersuchungen über die Organe der Lichtempfindungen bei niederen Thieren 1. Die Organe der Lichtempfindungen bei den Lumbriciden. Zeit. f. wiss. Zool., Bd. 62, pp. 393–419.

145. **Jennings, H. S.**, 1906. — Modifiability in Behavior, 2. Factors determining Direction and Character of Movement in the Earthworm. Journ. Exp. Zool., vol. 3, pp. 435–455.
146. **Johnston, J. B.**, 1903. — On the Blood Vessels, their Valves, and the Course of the Blood in Lumbricus. Biol. Bull., vol. 5, pp. 74–84.
147. **Langdon, F. E.**, 1895. — The Sense-Organs of Lumbricus agricola Hoffm. Journ. Morph., vol. 11, pp. 193–234.
148. **Marshall, A. M., and C. H. Hurst**, 1899. — Practical Zoology. 5th edition. New York.
149. **Morgan, T. H.**, 1901. — Regeneration. New York.
150. **Nagel, W. A.**, 1896. — Der Lichtsinn augenloser Thiere. Jena.
151. **Parker, G. H.**, 1909. — The Origin of the Nervous System and its Appropriation of Effectors. Pop. Sc. Monthly, vol. 75, pp. 56–64; 137–146; 253–263; 338–345.
152. ——, **and L. Arkin**, 1901. — The Directive Influence of Light on the Earthworm, Allolobophora fœtida. Am. Journ. Physiol., vol. 5, pp. 151–157.
153. ——, **and C. R. Metcalf**, 1906. — The Reactions of Earthworms to Salts. Am. Journ. Physiol., vol. 17, pp. 55–74.
154. **Rice, W. J.**, 1902. — Studies in Earthworm Chloragogue. Biol. Bull., vol. 3, pp. 88–94.
155. **Smith, A. E.**, 1902. — The Influence of Temperature, Odors, Light, and Contact on the Movements of the Earthworm. Am. Journ. Physiol., vol. 6, pp. 459–486.
156. **Washburn, M. F.**, 1908. — The Animal Mind. New York.
157. **Wilson, E. B.**, 1889. — The Embryology of the Earthworm. Journ. Morph., vol. 3, pp. 387–462.

CHAPTER XI

THE CRAYFISH AND ARTHROPODS IN GENERAL

158. **Andrews, E. A.**, 1904. — Crayfish Spermatozoa. Anat. Anz., Bd. 25, pp. 456–463.
159. ——, 1904. — Breeding Habits of Crayfish. Am. Nat., vol. 38, pp. 165–206.
160. ——, 1906. — Egg-laying of Crayfish. Am. Nat., vol. 40, pp. 343–356.
161. ——, 1906. — Partial Regeneration of the Sperm-receptacle in Crayfish. Journ. Exp. Zool., vol. 3, pp. 121–128.

162. ——, 1906. — The Future of the Crayfish Industry. Science. N. S., vol. 23, pp. 983–986.
163. ——, 1908. — The Young of the Crayfishes Astacus and Cambarus, Smithsonian Contrib. to Knowledge, vol. 35, 79 pp.
164. **Bell**, J. C., 1906. — The Reactions of the Crayfish. Harvard Psych. Studies, vol. 2, pp. 615–644.
165. ——, 1906. — The Reactions of the Crayfish to Chemical Stimuli. Journ. Comp. Neur. and Psych., vol. 16, pp. 299–326.
166. **Cambridge Natural History**, vol. 4, 1909. London.
167. **Chidester, F. E.**, 1908. — Notes on the Daily Life and Food of Cambarus bartonius bartoni. Am. Nat., vol. 42, pp. 710–716.
168. **Dearborn, G.**, 1900. — The Individual Psycho-physiology of the Crayfish. Am. Journ. Physiol., vol. 3, pp. 404–433.
169. **Faxon, W.**, 1885. — A Revision of the Astacidæ. Mem. Mus. Comp. Zool., vol. 10, 186 pp.
170. **Huxley, T. H.** — The Crayfish. New York.
171. **Korschelt, E., and K. Heider**, 1899. — Embryology of Invertebrates. Translated by M. Bernard. Edited by M. F. Woodward. London.
172. **Kreidl, A.**, 1893. — Weitere Beiträge zur Physiologie des Ohrlabyrinthes. Sitz. d. kais. Akad. d. wiss., Wien., 3 Abth., Bd. 102, pp. 149–175.
173. **Marshall, A. M., and H. H. Hurst**, 1899. — Practical Zoology. 5th edition. New York.
174. **Miller, W. S.**, 1895. — The Anatomy of the Heart of Cambarus. Wisc. Acad. Science, vol. 10, pp. 325–338.
175. **Montgomery, T. H.**, 1906. — The Analysis of Racial Descent in Animals. New York.
176. **Morgan, T. H.**, 1901. — Regeneration. New York.
177. ——, 1903. — Evolution and Adaptation. New York.
178. ——, 1904. — Germ Layers and Regeneration. Arch. Ent. mech. Bd. 18, pp. 261–264.
179. **Ortmann, A. E.**, 1907. — The Crayfishes of the State of Pennsylvania. Mem. Carnegie Mus., vol. 2, pp. 343–533.
180. **Parker, G. H.**, 1895. — The Retina and Optic Ganglia in Decapods, especially in Astacus. Mitth. Zool. Stat. z. Neapel, Bd. 12, pp. 1–73.
181. **Prentiss, C. W.**, 1901. — The Otocyst of Decapod Crustacea. Bull. Mus. Comp. Zool. Harvard, vol. 36, pp. 167–251.
182. **Reed, M.**, 1904. — The Regeneration of the First Leg of the Crayfish. Arch. Ent. mech., Bd. 18, pp. 307–316.
183. **Sedgwick, A.**, 1909. — Text-book of Zoology, vol. 3. London.

184. **Shull, C. A.**, 1909. — Some Abnormalities and Regeneration of Pleipods in Cambarus and other Decapoda. Biol. Bull., vol. 16, pp. 297–312.
185. **Treatise on Zoology**, ed. by E. R. Lankester, 1909. Vol. 7, 3d fascicle. London.
186. **Washburn, M. F.**, 1908. — The Animal Mind. New York.
187. **Weismann, A.**, 1904. — The Evolution Theory, vol. 2, translated by J. A. Thomson. London.
188. **Yerkes, R. M., and G. E. Huggins**, 1903. — Habit Formation in the Crawfish, Cambarus affinis. Harvard Psych. Studies, vol. 1, pp. 565–577.
189. **Zeleny, C.**, 1905. — The Relation of the Degree of Injury to the Rate of Regeneration. Journ. Exp. Zool., vol. 2, pp. 348–369.
190. ——, 1906. — The Regeneration of an Antennalike Organ in place of the Vestigial Eye of the blind Crayfish. Science, N. S., vol. 23, p. 527.

CHAPTER XII

THE HONEYBEE AND BEES IN GENERAL

191. **Benton, F.**, 1896. — The Honey Bee. Bull. 1, N. S. (Revised Edition), Div. Entomol., U. S. Dep't Agric., 118 pp.
192. ——, 1905. — Bee Keeping. Farmer's Bull., 59, U. S. Dep't Agric.
193. **Bonnier, G.**, 1901. — L'accoutumance des abeilles et la couleur des fleurs. C. r. Acad. Sci., Paris, tome 141, pp. 988–994.
194. ——, 1906. — Sur la Division du Travail chez les Abeilles. C. r. Acad. Sci., Paris, tome 143, pp. 941–946.
195. **Bresslau, E.**, 1905. — Der Samenblasengang der Beinenkönigin. Zool. Anz., Bd. 29, pp. 299–323.
196. **Buttel-Reepen, H. von**, 1900. — Sind die Bienen Reflexmaschine? Biol. Cent., Bd. 20, pp. 97–109; 130–144; 177–193; 209–224; 289–304.
197. **Cambridge Natural History**, 1899, vol. 6. London.
198. **Cheshire, F. R.**, 1886. — Bees and Bee-Keeping. 2 vols. London.
199. **Comstock, J. H., and A. B. Comstock**, 1907. — Manual for the Study of Insects, 7th ed. Ithaca.
200. **Cowan, T. W.**, 1904. — The Honey Bee. 2d ed. London.
201. **Dickel, F.**, 1908. — Zur Frage nach der Geschlechtsbestimmung der Honigbiene. Zool. Anz., Bd. 33, pp. 222–236; Bd. 34, 1909, pp. 212–223; 236–248.
202. **Dreyling, L.**, 1905. — Die Wachsbereitenden Organe bei den gesellig

lebenden Bienen. Zool. Jahrb., Abth. Morph., Bd. 22, pp. 289-330.
203. **Gibson, W. H.**, 1898. — My Studio Neighbors. New York.
204. **Graenicher, S.**, 1909. — Wisconsin Flowers and their Pollination. Bull. Wisc. Nat. Hist. Soc., vol. 7, pp. 19-77.
205. **Kathariner, L.**, 1903. — Versuche über die Art der Orientierung bei der Honigbiene. Biol. Centr., bd. 23, pp. 646-660.
206. **Kellogg, V. L.**, 1903. — Some Insect Reflexes. Science, N. S., vol. 18, pp. 693-696.
207. ——, 1905. — American Insects. New York.
208. **Lovell, J. H.**, 1909. — The Color Sense of the Honey Bee — Is conspicuousness an advantage to flowers? Am. Nat., vol. 43, pp. 338-349.
209. **Mark, E. L., and M. Copeland**, 1906. — Some Stages in the Spermatogenesis of the Honey Bee. Proc. Am. Acad. Arts and Sci., vol. 42, pp. 103-112.
210. **Meves, F.**, 1907. — Die Spermatocytentheilungen bei der Honeybiene (Apis mellifica L), nebst Bemerkungen über Chromatinreduction. Arch. Mikr. Anat., Bd. 70, pp. 414-491.
211. **Morgan, T. H.**, 1907. — The Cause of Gynandromorphism in Insects. Am Nat., vol. 41, pp. 715-718.
212. ——, 1907. — Experimental Zoology. New York.
213. **Mueller, H.**, 1873. — Die Befruchtung der Blumen durch Insekten.
214. **Packard, A. S.**, 1903. — Text-Book of Entomology. New York.
215. **Petrunkewitsch, A.**, 1901. — Die Richtungskörper und ihr Schicksal im befruchteten und unbefruchteten Bienenei. Zool. Jahrb. Abth. Morph., Bd. 14, pp. 291-310.
216. **Phillips, E. F.**, 1905. — Structure and Development of the Compound Eye of the Honey Bee. Proc. Acad. Nat. Sci. Philad., vol. 57, pp. 123-157.
217. **Plateau, F.**, 1907. — Les insectes et la couleur des fleurs. L'Ann. Psych., tome 13, pp. 67-79.
218. **Root, A. I., and E. R. Root**, 1908. — The A B C and X Y Z of Bee Culture. Medina.
219. **Sedgwick, A.**, 1909. — Text-book of Zoology, vol. 3. London.

CHAPTER XIII

HISTORICAL ZOOLOGY

220. **Hertwig, R.**, 1902. — Manual of Zoology. Translated and edited by J. S. Kingsley. New York.

221. **Locy, W. A.**, 1908. — Biology and its Makers. New York.
222. **Osborn, H. F.**, 1894. — From the Greeks to Darwin. New York.
223. **Parker, T. J., and W. A. Haswell**, 1897. — Text-book of Zoology, vol. 2. London.
224. **Thompson, J. A.**, 1899. The Science of Life. London.

CHAPTER XIV

GENERAL CONSIDERATIONS OF ZOOLOGICAL FACTS AND THEORIES

225. **Adams, C. C.**, 1902. — Southeastern United States as a Center of Geographical Distribution of Flora and Fauna. Biol. Bull., vol. 3, pp. 115–131.
226. **Baldwin, J. M.**, 1902. — Dictionary of Philosophy and Psychology, 3 vols. New York.
227. **Bateson, W.**, 1902. — Mendel's Principles of Heredity, a Defence. Cambridge.
228. **Beddard, F. E.**, 1895. — A Text-book of Zoogeography. Cambridge.
229. **Bethe, A.**, 1898. — Dürfen wir den Ameisen u. Bienen Psychische Qualitäten zuschreiben? Pflügers Arch., Bd. 70, pp. 15–100.
230. **Brooks, W. K.**, 1883. — The Law of Heredity. Baltimore.
231. ——, 1899. — The Foundations of Zoology. New York.
232. **Conn, H. W.**, 1903. — The Method of Evolution. New York.
233. **Cope, E. D.**, 1896. — The Primary Factors of Organic Evolution. Chicago.
234. **Cunningham, J. T.**, 1892. — The Evolution of Flat Fishes. Nat. Sci., vol. 1, pp. 191–195; vol. 6, pp. 169–177, 233–238.
235. **Darwin, Charles**, 1890. — Journal of Researches during the Voyage round the World in H. M. S. *Beagle*, 2d ed. New York.
236. ——, 1886. — On the Origin of Species by Means of Natural Selection. New York.
237. **Delage, Y.**, 1884. — Évolution de la Sacculine. Arch. zool. expér. gén., ser. 2, tome 2.
238. ——, 1903. — L'herédité et les grands problèmes de la biologie générale. 2me ed. Paris.
239. **Eimer, G. H. Th.**, 1890. — Organic Evolution. London.
240. **Forel, A.**, 1904. — Ants and Some Other Insects. Translated by W. M. Wheeler. Chicago.
241. **Galton, F.**, 1897. — The Average Contribution of Each Several Ancestor to the Total Heritage of the Offspring. Proc. Roy. Soc., London, vol. 61, pp. 401–413.

242. **Haeckel, Ernst**, 1883. — The Evolution of Man. 2 vols.
243. **Headley, F. W.**, 1900. — Problems of Evolution. London.
244. **James, W.**, 1890. — The Principles of Psychology. 2 vols. New York.
245. **Jennings, H. S.**, 1904. — Contributions to the Study of the Behavior of Lower Organisms. Carnegie Inst. Pub. Washington.
246. ——, 1906. — Behavior of the Lower Organisms. New York.
247. ——, 1908. — The Interpretation of the Behavior of the Lower Organisms. Science, N. S., vol. 27, pp. 698–710.
248. **Jordan, D. S.**, 1905. — The Origin of Species through Isolation. Science, N. S., vol. 22, pp. 545–562.
249. ——, **and V. L. Kellogg**, 1907. — Evolution and Animal life. New York.
250. **Kellogg, V. L.**, 1907. — Darwinism To-Day. New York.
251. **Loeb, J.**, 1900. — Comparative Physiology of the Brain and Comparative Psychology. New York.
252. ——, 1905. — Studies in General Physiology, 2 pts. Chicago.
253. ——, 1906. — The Dynamics of Living Matter. New York.
254. ——, 1907. — Concerning the Theory of Tropisms. Journ. Exp. Zool., vol. 4, pp. 151–156.
255. **Merriam, C. H.**, 1898. — Life Zones and Crop Zones of the United States. Bull. 10, Biol. Survey, U. S. Dep't of Agric.
256. **Metcalf, M. M.**, 1904. — Organic Evolution. New York.
257. **Montgomery, T. H.**, 1906. — Analysis of Racial Descent in Animals. New York.
258. **Morgan, C. L.**, 1896. — Habit and Instinct. London.
259. ——, 1908. — Animal Behavior, 2d ed. New York.
260. **Morgan, T. H.**, 1903. — Evolution and Adaptation. New York.
261. ——, 1907. — Experimental Zoology. New York.
262. **Müller, F.**, 1864. — Für Darwin. Leipzig.
263. **Osborn, H. F.**, 1908. — The Four Inseparable Factors of Evolution. Science, N. S., vol. 27, pp. 148–150.
264. **Plate, L.**, 1903. — Ueber die Bedeutung der Darwin'schen Selectionsprinzip.
265. **Romanes, J. G.**, 1892–1897. — Darwin and after Darwin. 3 vols. London.
266. **Ruthven, A. G.**, 1908. — Variations and Genetic Relationships of the Garter Snakes. Bull. 61, U. S. Nat. Mus.
267. **Stevens, W. C.**, 1902. — Introduction to Botany. Boston.
268. **Thomson, J. A.**, 1896. — The Study of Animal Life. New York.
269. ——, 1908. — Heredity. New York.

270. **Tower, W. L.**, 1906. — Evolution in Chrysomelid Beetles of the Genus Leptinotarsa. Carnegie Inst. Pub. Washington.
271. **Van Beneden, E.**, 1889. — Animal Parasites and Messmates.
272. **Vries, H. de**, 1905. — Species and Varieties, their Origin by Mutation. Chicago.
273. **Wallace, A. R.**, 1876. — The Geographical Distribution of Animals. London.
274. ——, 1881. — Island Life. London.
275. ——, 1903. — Darwinism. London.
276. **Washburn, M. F.**, 1908. — The Animal Mind. New York.
277. **Wasmann, E.**, 1903. — Instinct and Intelligence in the Animal Kingdom. St. Louis.
278. **Weismann, A.**, 1904. — The Evolution Theory. 2 vols. London.
279. **Weysse, A. W.**, 1904. — A Synoptic Text-book of Zoology. New York.
280. **Whitman, C. O.**, 1906. — The Problem of the Origin of Species. Proc. Cong. Arts and Sci., Universal Exposition, St. Louis, vol. 5, pp. 41–58.

GLOSSARY *

KEY TO PRONUNCIATION

a *as in* mat, man.	o *as in* not, on.
ā *as in* mate, dale.	ō *as in* note, soul.
ä *as in* far, father.	ö *as in* move, spoon.
â *as in* fall, law.	ô *as in* nor, song.
e *as in* met, pen.	u *as in* tub, son.
ē *as in* free, meet.	ū *as in* due, mute.
ė *as in* her, fern.	
i *as in* tin, it.	
ī *as in* tie, pie.	

abdomen, *ab dō'men* (L. *abdōmen,* the belly — from *abdo,* I conceal), the lower belly.

absorption, *ab sôrp'shon* (L. *absorbēre,* swallow down anything), the process of taking up, as by chemical or molecular action.

accretion, *a krē'shon* (L. *ad,* to ; *cretum,* to grow), growth by external addition of new matter.

achromatin, *a krō'ma tin* (Gr. *a,* without ; *chroma,* color), the non-staining substance of the nucleus.

acœlomate, *a sē'lō māt* (Gr. *a,* without ; *koilos,* hollow), without a true body cavity or cœlom.

afferent, *af'e rent* (L. *affĕro,* I bring to), conveying from the surface to the center.

ameba, *a mē'bä* (Gr. *amoibos,* change), a genus of rhizopodous Protozoa.

amitosis, *a mi tō'sis* (Gr. *a,* without ; *mitos,* a thread), direct nuclear division without the formation of chromosomes and amphiaster.

amphiaster, *am'fi as tėr* (Gr. *amphi,* around ; *aster,* a star), the achromatic figure formed in mitotic cell division, consisting of two asters connected by a spindle.

anabolism, *an ab'ō lizm* (Gr. *anabole,* a throwing up), constructive metabolism.

analogous, *a nal'ō gus* (Gr. *ana,* similar to; *logos,* proportion), like in function, but not in structure.

* *The Century Dictionary and Cyclopedia,* the Rev. James Stormonth's *Manual of Scientific Terms,* and E. B. Wilson's *Cell in Development and Inheritance* have been invaluable in preparing this glossary.

anaphase, *an'a fāz* (Gr. *ana*, back or again), the later period of mitosis during the divergence of the daughter chromosomes.

anatomy, *a nat'ō mi* (Gr. *anatemno*, to cut up), the study of the structure of organisms as made out by dissection.

Annelida, *a nel'i dä* (L. *annellus*, a little ring; Gr. *eidos*, resemblance), a phylum of animals having bodies made up of many small rings.

antenna, *an ten'ä* (L. *antenna*, a sail yard), the jointed feelers upon the heads of insects and crustaceans.

antennule, *an ten'ūl* (L. dim. of *antenna*), the smaller pair of antennæ in the crustaceans.

anus, *ā'nus* (L. *ānus*, a ring), the orifice through which the refuse of digestion is voided.

Apis, *ā'pis* (L. *apis*, a bee), a genus of bees.

archenteron, *är ken'te ron* (Gr. *archē*, beginning; *enteron*, intestine), the primitive digestive cavity.

arthrobranchia, *är thrō brang'ki ä* (Gr. *arthron*, a joint; *brangchia*, the gill of a fish), part of the respiratory system of the crayfish.

Arthropoda, *är throp'ō dä* (Gr. *arthron*, a joint; *pous*, foot), a phylum of animals having bodies composed of segments, some or all of which bear jointed appendages.

Ascaris, *as'ka ris* (Gr. *askaris*, a worm in the intestines), a genus of round worms.

asexual, *a sek'sū al* (Gr. *a*, without; and *sexual*), applied to modes of reproduction in which the sexes are not concerned.

assimilation, *a sim i lā'shon* (L. *assimilo*, to make like), the conversion of digested food into living protoplasm.

aster, *as'tẽr* (Gr. *aster*, a star), the star-shaped structure surrounding the centrosome.

auditory, *â'di tō ri* (L. *auditor*, a hearer), pertaining to the sense of hearing.

behavior, *bē hāv'yor* (*be*, about; *habban*, hold, have), the sum total of all the various movements of an animal.

bilateral, *bī lat'e ral* (L. *bis*, twice; *lăteris*, of a side), having the sides symmetrical.

biogenesis, *bī ō jen'e sis* (Gr. *bios*, life; *genesis*, origin), the genesis of living beings from living beings.

biology, *bī ol'ō ji* (Gr. *bios*, life; *logos*, discourse), the science of life and living things.

biramous, *bī rā'mus* (L. *bi*, two; *ramus* a branch), dividing into two branches.

blastocœl, *blas'tō sēl* (Gr. *blastos*, a bud; *koilos*, a hollow), the cavity of the blastula.

blastoderm, *blas'tō dĕrm* (Gr. *blastos,* a bud; *derma,* skin), the layer of cells forming the wall of the blastula.

blastomere, *blas'tō mēr* (Gr. *blastos,* a bud; *meros,* a part), a term applied to a cell during cleavage of the egg.

blastopore, *blas'tō pōr* (Gr. *blastos,* a bud; *poros,* pore), the opening of the gastrula, the primitive mouth.

blastula, *blas'tū lă* (dim. of Gr. *blastos,* a bud), an embryo consisting of a sac formed of a single layer of cells.

botany, *bot'a ni* (Gr. *botane,* a plant), the science which treats of plants.

branchial, *brang'kial* (L. *branchiæ,* gills), pertaining to the gills.

buccal, *buk'al* (L. *bucca,* a cheek), pertaining to the cheek or mouth.

Cambarus, *kam'ba rus* (L. *camarus,* a sea crab), a genus of crayfishes.

capillary, *kap'i lā ri* (L. *capillus,* hair), a hairlike tube.

carapace, *kar'a pās* (Gr. *karabos,* a crustaceous animal like the crab), the shield covering the cephalothorax of the crayfish.

carbohydrate, *kär bō hī'drāt* (L. *carbo,* a coal; Gr. *hudor,* water), an organic body containing 6 carbon atoms or some multiple of 6, and hydrogen and oxygen in the proportion in which they form water (H_2O).

cardiac, *kär'di ak* (Gr. *kardia,* the heart), pertaining to the heart.

caudal, *kâ'dal* (L. *cauda,* a tail), having a position or relation toward the tail when compared with some other part.

cell, *sel* (L. *cella,* a store-room), a mass of protoplasm containing a nucleus; the unit of structure of the Metazoa.

centrosome, *sen'trō sōm* (Gr. *centron,* center; *soma,* body), a body found at the center of the aster of the amphiaster during mitotic cell division.

cephalic, *se fal'ik* (Gr. *kephale,* the head), having a position or relation toward the head when compared with some other part.

cephalothorax, *sef'a lō thō'raks* (Gr. *kaphale,* the head; *thorax,* the thorax), the (coalesced) head and thorax of certain arthropods.

cervical, *sėr'vi kal* (L. *cervix,* the neck), of or pertaining to the neck.

chela, *kē'lă* (Gr. *kele,* a claw), the pair of pinchers that terminates some of the appendages of certain crustaceans.

cheliped, *kē'li ped* (Gr. *kele,* a claw; L. *pes,* foot), the chelate walking legs of the crayfish and other crustaceans.

chemotropism, *kem ot'rō pism* (Gr. *chemeia,* a mingling; *trope,* a turning), the reaction of an animal to a chemical.

chitin, *kī'tin* (Gr. *chiton,* a coat of mail), the organic substance forming the exoskeleton of arthropods and certain other animals.

chlorogogen, *klō'rō gō'jen* (Gr. *chloros,* grass-green), (see p. 169).

chlorophyll, *klō'rō fil* (Gr. *chloros,* grass-green; *phullon,* a leaf), the green coloring matter of plants.

choanocyte, *kō'a nō sīt* (Gr. *choane,* a funnel; *kutos,* a cavity), a collared cell of the sponge.

chromatin, *krō'ma tin* (Gr. *chroma,* color), the deeply staining substance of the nuclear network and of the chromosomes, consisting of nuclein.

chromosome, *krō'mō sōm* (Gr. *chroma,* color; *soma,* body), the deeply staining bodies into which the chromatic nuclear network resolves itself during mitosis.

chromotropism, *krō mŏt'rō pizm* (Gr. *chroma,* color; *trope,* a turning), the reaction of an animal to color.

cilium, *sil'i um* (L. *cilium,* an eyelid with the hairs growing on it), a minute hairlike process of a cell.

class, *klȧs* (L. *classis,* an assembly of people), a number of animals regarded as a collective unit because of the presence of certain common characters.

cleavage, *klē'vāj,* the division of the fertilized egg.

clitellum, *kli tel'um* (L. *clitellæ,* a pack saddle), a glandular ring around the body of the earthworm.

cnidoblast, *nī'dō blȧst* (Gr. *knide,* a nettle; *blastos,* a bud), a cell in which a nematocyst is developed.

cnidocil, *nī'dō sil* (Gr. *knide,* a nettle; L. *cilium,* an eyelid), a stiff hairlike process projecting from a cnidoblast.

coagulate, *kō ag'ū lāt* (L. *coagulare,* curdle), change from a fluid into a curdlike or thickened mass.

Cœlentera, *sē len'te rä* (Gr. *koilos,* hollow; *enteron,* intestine), a phylum of animals with a single body cavity which opens by a single orifice, the mouth.

cœlom, *sē'lom* (Gr. *koilos,* hollow), the true body cavity, lying between the digestive tract and the body wall, and lined with epithelium.

cœlomate, *sē lō'māt* (Gr. *koilos,* hollow), having a cœlom.

commensalism, *ko men'sal izm* (L. *com,* together; *mensa,* table), the living together of two species of animals or plants, but neither at the expense of the other.

conjugation, *kon jö gā'shon* (L. *conjugatum,* to unite), a temporary or permanent union of two cells for reproduction.

contractility, *kon trak til'i ti* (L. *contractus,* a drawing together), the property or force by which bodies shrink or contract.

copulation, *kop ū lā'shon* (L. *copulare,* unite), the active transmission of sperm from the male to the female.

cortical, *kôr'ti kal* (L. *cortex,* bark, rind), belonging to the external covering.

cuticle, *kū'ti kl* (L. *cuticula,* dim. of *cutis,* the skin), the outermost covering of the body of certain animals.

cyclosis, *sī klō'sis* (Gr. *kuklos,* a circle), applied to currents within the bodies of Protozoa.

cyst, *sist* (Gr. *kustis*, a bladder), a term applied to certain Protozoa when they surround themselves with a wall and pass into a resting stage.

cytopharynx, *sī'tō far'ingks* (Gr. *kutos*, a vessel; *pharungx*, gullet), a tube leading from the bottom of the oral groove into the body of a Paramecium.

cytoplasm, *sī'tō plazm* (Gr. *kutos*, a vessel; *plasma*, anything formed), the substance of the cell body as opposed to that of the nucleus.

diastase, *dī'a stās* (Gr. *diastasis*, a separation), a substance which has the property of converting starch into sugar.

diastole, *dī as'tō lē* (Gr. *diastole*, separation), the period of time during which a rhythmically pulsating vessel is relaxed or dilated.

digestion, *di jes'tyon* (L. *digestio*, the dissolving of food), the process of preparing food for absorption.

diœcious, *dī ē'shus* (Gr. *dis*, twice; *oikos*, a house), having the sexes distinct, applied to species that consist of male and female individuals.

diploblastic, *dip lō blas'tik* (Gr. *diploos*, double; *blastos*, a bud), having two germinal layers.

dissimilation, *di sim i lā'shon* (L. *dissimilare*, make unlike), the processes by which protoplasm is broken down into simpler products.

distal, *dis'tal* (L. *disto*, I stand apart), situated away from the place of attachment.

dorsal, *dôr'sal* (L. *dorsum*, the back), of or pertaining to the back.

ecdysis, *ek di sis* (Gr. *ekdusis*, emerging), shedding or molting the external covering.

ectoderm, *ek'tō derm* (Gr. *ektos*, outside; *derma*, skin), the outer germ layer.

ectosarc, *ek'tō särk* (Gr. *ektos*, outside; *sarx*, flesh), the outer layer of certain Protozoa.

efferent, *ef'e rent* (L. *ef* for *ex*, out; *fero*, I carry), conveying outward.

egestion, *ē jes'chon* (L. *egestio*, void), the act of voiding the refuse of digestion.

electrotropism, *ē lek'trō trō pizm* (Gr. *elektron*, amber; *trope*, a turning), reaction to the electric current.

embryo, *em'bri ō* (Gr. *en*, in; *bruo*, bud), the early stage of an animal when it is within the egg membrane.

endopodite, *en dop'ō dīt* (Gr. *endon*, within; *pous*, a foot), the inner of the two main divisions of a typical crustacean appendage.

endosarc, *en'dō särk* (Gr. *endon*, within; *sarx*, flesh), the inner protoplasm of certain Protozoa.

enteron, *en'te ron* (Gr. *enteron*, intestine), the digestive tract that is primitively derived from the entoderm.

entoderm, *en'tō derm* (Gr. *endon*, within; *derma*, skin), the inner germ layer.

enzyme, *en'zim* (Gr. *en*, in; *zume*, leaven), an unorganized ferment.

epigenesis, *ep i jen'e sis* (Gr. *epi*, upon; *genesis*), a theory of development (see p. 272).

epipodite, *e pip'ō dīt* (Gr. *epi*, upon; *pous*, foot), a process developed upon the basal joint of some of the appendages of certain crustaceans.

epithelium, *ep i thē'li um* (Gr. *epi*, upon; *thallo*, I grow), the layer of cells forming the surface of all the internal membranes of the body.

evolution, *ev ō lū'shon* (L. *e*, out; *volvo*, roll), a theory of development (see p. 291).

excretion, *eks krē'shon* (L. *ex*, out; *cretus*, separated), the elimination of useless or harmful substances from the body.

exopodite, *ek sop'ō dīt* (Gr. *exo*, outside; *pous*, foot), the outer of the two main divisions of a typical crustacean appendage.

exoskeleton, *ek sō skel'e ton* (Gr. *exo*, outside; *skeleton*), any structure produced by the hardening of the integument.

fæces, *fē'sēs* (L. *fæx*, dregs), undigested particles cast out by an animal.

family, *fam'i li* (L. *familia*, a household), the name of a group above a genus and below an order.

fauna, *fâ'nä* (L. *Faunus*, one of the gods of the fields), all the animals peculiar to a country, area, or period.

ferment, *fėr'ment* (L. *fermentum*, leaven), a substance which transforms an organic substance into new compounds.

fertilization, *fėr'ti li zā'shon* (L. *fertilis*, fruitful), the union of a spermatozoon with an egg.

flagellum, *flā jel'um* (L. *flagellum*, a whip), the whiplike appendage of many Protozoa.

foliaceous, *fō li ā'shius* (L. *folium*, leaf) resembling a leaf.

function, *fungk'shon* (L. *functio*, performance), the mode of action proper to an organ or structure.

gamete, *gam'ēt* (Gr. *gamete*, a wife), a reproductive cell which unites with another reproductive cell to form a zygote.

ganglion, *gang'gli on* (Gr. *ganglion*, a tumor under the skin near a tendon), a mass of nervous tissue containing nerve cells and giving rise to nerve fibers.

gastric, *gas'trik* (Gr. *gaster*, stomach), of or pertaining to the stomach.

gastrolith, *gas'trō lith* (Gr. *gaster*, stomach; *lithos*, stone), a stony concretion in the stomach of certain crustaceans.

gastrula, *gas'trö lä* (dim. of Gr. *gaster*, stomach), an embryo consisting of two germ layers inclosing a central cavity.

genital, *jen'i tal* (L. *genitalis*, serving to beget), pertaining to the organs of generation.

genus, *jē'nus* (L. *genus*, race), a group containing one or more species.

geotropism, *jē ot'rō pizm* (Gr. *gea*, earth; *trope*, a turning), reaction to gravity.

germ cell, *jėrm' sel* (L. *germen*, bud; *cella*, store room), a reproductive cell.

germ layer, *jerm' lā'er* (L. *germen*, bud), one of the fundamental embryonic membranes from which the organs of the body arise.

germ plasm, *jerm'pla'zm* (L. *germen*, bud; Gr. *plasma*, a thing molded), the protoplasm of the germ cells.

gullet, *gul'et* (F. *goule*, mouth), something resembling the throat in shape position, or functions.

gynandromorph, *ji nan'drō mŏrf* (Gr. *gunandros*, of doubtful sex; *morphe*, form), an animal with both male and female characters.

hæmoglobin, *hĕm ō glō'bin* (Gr. *haima;* L. *globus*, ball), the red coloring matter in the blood of certain animals.

hepatic, *hē pat'ik* (Gr. *hepar*, liver), of or pertaining in any way to the liver.

heredity, *hē red'i ti* (L. *heres*, an heir), the resemblance of child to parent.

hermaphrodite, *hėr maf'rō dīt* (Gr. *Hermes*, the god mercury; *Aphrodite*, the goddess Venus), an animal possessing the reproductive organs of both male and female.

heteromorphosis, *het'e rō mŏrf'ō sis* (Gr. *heteros*, different; *morphe*, form), in regeneration, the production of a new part unlike that removed.

histology, *his tol'ō ji* (Gr. *histos*, tissue; *logos*, discourse), the study of the microscopic structure of tissues.

holoblastic, *hōl ō blas'tik* (Gr. *holos*, whole; *blastos*, germ), applied to eggs with total cleavage.

holophytic, *hōl ō fit'ik* (Gr. *holos*, whole; *phuton*, a plant), resembling a plant in mode of nutrition.

holozoic, *hōl ō zō'ik* (Gr. *holos*, whole; *zoon*, an animal), resembling an animal in mode of nutrition.

homologous, *hō mol'ō gus* (Gr. *homos*, like; *logos*, speech), having the same relative position or structure, *i.e.* anatomically similar.

Hydra, *hī drā* (L. *hydra*, a water snake), a genus of fresh water polyps.

hypodermis, *hy po der'mis* (Gr. *hupo*, under; *derma*, skin), the layer of cells just below the cuticle of certain animals.

hypostome, *hī'pō stōm* (Gr. *hupo*, under; *stoma*, a mouth), a structure near the mouth of certain cœlenterates and crustaceans.

ingestion, *in jes'chon* (L. *ingestus*, poured into), the introduction of food into the body.

interstitial, *in tėr stish'al* (L. *inter*, between; *sisto*, I stand), pertaining to or situated in an intervening space.

intracellular, *in trā sel'ū lār* (L. *intra*, within), existing or done inside of a cell.

intussusception, *in'tu su sep'shon* (L. *intus*, within; *susceptus*, taken up), the addition of new particles among the preexisting particles of protoplasm.

irritability, *ir'i ta bil'i ti* (L. *irritare*, excite), the property of responding to stimuli.

karyoplasm, *kar'i ō plazm* (Gr. *karuon*, nucleus; *plasma*, a thing formed), the substance of the nucleus.

karyosome, *kar'i ō sōm* (Gr. *karuon*, nucleus; *soma*, body), nucleoli which stain with nuclear dyes.

katabolism, *ka tab'ō lizm* (Gr. *katabole*, a throwing down), the process by which protoplasm breaks down into simpler products.

larva, *lär'vä* (L. *larva*, a ghost or mask), the young of any animal which during its development is unlike its parent.

lateral, *lat'e ral* (L. *latus*, side), of or pertaining to the side.

Lumbricus, *lum brī'kus* (L. *lumbricus*, earthworm), a genus of worms.

macrogamete, *mak'rō gam'ēt* (Gr. *makros*, long; *gamete*, wife), a large reproductive cell, the egg.

macromere, *mak'rō mēr* (Gr. *makros*, long; *meros*, a part), the larger cells in the early embryonic stages of certain animals.

macronucleus *mak rō nū'klē us* (Gr. *makros*, long; *nucleus*), a large nucleus in certain Protozoa.

maturation, *mat ū rā'shon* (L. *maturare*, ripen), the ripening of the egg by the formation of polar bodies.

maxilla, *mak sil'ä* (L. *maxilla*, a jaw), an appendage near the mouth of arthropods.

maxilliped, *mak sil'i ped* (L. *maxilla*, a jaw; *pedes*, foot), a footlike appendage near the mouth of certain arthropods.

medusa, *mē dū'sä* (L. *Medusa*, a mythological woman whose hair was turned into snakes), a jellyfish, or reproductive zooid of certain cœlenterates.

meroblastic, *mer ō blas'tik* (Gr. *meros*, a part; *blastos*, a germ), applied to eggs only part of which are cut up into cells during cleavage.

mesoderm, *mes'sō dėrm* (Gr. *mesos*, middle; *derma*, skin), the middle germ layer of triploblastic animals.

mesoglea, *mes ō glē'ā* (Gr. *mesos*, middle; *gloia*, glue), the gelatinous substance between the ectoderm and entoderm of cœlenterates.

metabolism, *me tab'ō lizm* (Gr. *metabole*, change), the processes connected with the manufacture and destruction of protoplasm.

metamere, *met'a mēr* (Gr. *meta,* after; *meros,* a part), one of a longitudinal series of parts which are serially homologous with one another.

metamorphosis, *met a môr'fō sis* (Gr. *meta,* change; *morphe,* shape), a marked change in form or function.

metaphase, *met'a fāz* (Gr. *meta,* after), the middle stage of mitosis during which occurs the splitting of the chromosomes in the equatorial plate.

metaplasm, *met'a plazm* (Gr. *meta,* after; *plasma,* a thing formed), applied to lifeless inclusions in protoplasm.

Metazoa, *met a zō'ä* (Gr. *meta,* after; *zoon,* an animal), many-celled animals.

microgamete, *mī krō gam'ēt* (Gr. *mikros,* small; *gamete,* a wife), a small reproductive cell, the spermatozoon.

micromere, *mī'krō mēr* (Gr. *mikros,* small; *meros,* a part), the smaller cells in the embryonic stages of certain animals.

micronucleus, *mī krō nū'klē us* (Gr. *mikros,* small; *nucleus*), the smaller of two nuclei in certain Protozoa.

mitosis, *mī tō'sis* (Gr. *mitos,* a thread), indirect nuclear division.

monœcious, *mō nē'shus* (Gr. *monos,* one; *oikos,* a house), having both male and female sexual organs.

morphology, *môr fol'ō ji* (Gr. *morphe,* form; *logos,* description), the science of form and structure.

moult, *mōlt* (L. *mutare,* change), the process of casting off tegumentary, cuticular, or exoskeletal structures.

mutation, *mū tā'shon* (L. *mutare,* change), a theory of the origin of species (see p. 295).

nematocyst, *nem'a tō sist* (Gr. *nema,* thread; *kustis,* a bag), a structure containing a thread, characteristic of cœlenterates.

nephridium, *ne frid'i um* (Gr. *nephros,* a kidney), one of the excretory organs of the earthworm.

neuron, *nū'ron* (Gr. *neuron,* a nerve), a nerve cell with all its prolongations.

nucleolus, *nū klē'ō lus* (L. *nucleus,* a small nut), a deeply staining body often present within a nucleus.

nucleus, *nū'klē us* (L. *nucleus,* a small nut), the dynamic center of a cell.

nutriment, *nū'tri ment* (L. *nutrire,* nourish), that which promotes the growth or repairs the waste of animal bodies.

nutrition, *nū trish'on* (L. *nutrire,* nourish), the processes by which organisms take in food and add it to their living tissues.

ocellus, *ō sel'us* (L. *ocellus,* a little eye), a simple eye of an insect.

œsophagus, *ē sof'a gus* (Gr. *oisophagos,* the gullet), the canal through which food and drink passes to the stomach.

ommatidium, *om a tid'i um* (Gr. dim. of *omma,* eye), part of the compound eye of an arthropod.

ontogeny, *on toj'e ni* (Gr. *on,* being; *gennao,* I produce), the development of an individual organism.

oocyte, *ō'ō sīt* (Gr. *oon,* an egg), a stage in the maturation of an egg.

oogenesis, *ō ō jen'e sis* (Gr. *oon,* an egg; *genesis,* origin), the origin and development of the egg.

oogonium, *ō ō gō'ni um* (Gr. *oon,* an egg; *gonos,* generation), an egg just before maturation takes place.

organ, *ôr'gan* (L. *organum,* an instrument), a part of a organism having a specific function.

orthogenesis, *ôr thō jen'ē sis* (Gr. *orthos,* straight; *genesis*), a theory of evolution (see p. 294).

osculum, *os'kū lum* (L. *osculum,* a little mouth), an opening through which water is expelled from a sponge.

ostium, *os'ti um* (L. *ostium,* an opening), an opening in various organs of the body.

ovary, *ō'va ri* (L. *ovum,* an egg), the organ of the female in which eggs develop.

oviduct, *ō'vi dukt* (L. *ovum,* an egg; *ductus,* led), the duct of the ovary.

ovum, *ō'vum* (L. *ovum,* an egg), an egg.

oxidation, *ok si dā' shon* (Gr. *oxus,* sharp), the combination of a substance with oxygen.

paleontology, *pā'lē on tol'ō ji* (Gr. *palaios,* ancient; *onta,* beings; *logos,* discourse), the science of fossil organisms.

parasite, *par'a sīt* (Gr. *parasitos,* one who eats at another's expense), an animal that lives in, on, or at the expense of another animal.

parietal, *pā rī'e tal* (L. *paries,* wall), pertaining to the walls.

parthenogenesis, *pär'the nō jen'e sis* (Gr. *parthenos,* a virgin; *gennao,* I produce), reproduction by means of unfertilized eggs.

pellicle, *pel'i kl* (L. *pellicula,* a small skin), a thin outer covering of skin or cuticle.

pericardium, *per i kär'di um* (Gr. *peri,* round about; *kardia,* the heart), a membranous sac surrounding the heart.

peristaltic, *per i stal'tik* (Gr. *peristaltikos,* drawing together all round), applied to the waves of contraction running down the alimentary canal.

peristome, *per'i stōm* (Gr. *peri,* round about; *stoma,* a mouth), the part which surrounds the mouth or oral opening.

peritoneum, *per'i tō nē'um* (Gr. *peritonaion,* what is stretched round or over), the membrane lining the body cavity and covering most of the organs in the abdomen.

pharynx, *far'ingks* (Gr. *pharungx,* the gullet or windpipe), a part of the alimentary canal between the mouth and œsophagus.

photosynthesis, *fō tō sin'the sis* (Gr. *phos,* light; *synthesis,* a putting together), the manufacture of starch by chlorophyll in the presence of light.

phototropism, *fō tot'rō pizm* (Gr. *phos,* light; *trope,* a turning), reaction to light.

phylogeny, *fī loj'e ni* (Gr. *phylon,* a tribe; *gennao,* I produce), the study of the ancestral history of organisms.

phylum, *fī'lum* (Gr. *phylon,* a tribe), any primary division of the animal or vegetable kingdom.

physiology, *fiz i ol'ō ji* (Gr. *phusis,* nature; *logos,* discourse), the study of the functions of living things.

plasma, *plas'mä* (Gr. *plasma,* a thing formed), protoplasm; the liquid part of the blood.

plasmosome, *plas'mō zōm* (Gr. *plasma,* a thing formed; *soma,* body), a nuclear constituent distinguished by its affinity for plasma-stains.

plastid, *plas'tid* (Gr. *plasso,* I form or mold), a permanent cell organ other than nucleus and centrosome.

pleopod, *plē'ō pod* (Gr. *pleein,* swim; *pous,* foot), one of the abdominal appendages of a crustacean; swimmeret.

polar bodies, two minute cells segmented off from the ovum before union of the germ nuclei.

pollen, *pol'en* (L. *pollen,* fine flour), the fertilizing powder contained in the anthers of flowers.

pronucleus, *prō nū'klē us* (L. *pro,* before; *nucleus*), a male or female nucleus during fertilization.

prophase, *prō'fāz* (Gr. *pro,* before), the early period of mitosis.

propolis, *prop'ō lis* (Gr. *pro,* before; *polis,* city), a substance collected by bees to stop up crevices in the hive.

prostomium, *prō stō'mi um* (Gr. *pro,* before; *stoma,* mouth), the region in front of the mouth.

proteid, *prō'tē id* (Gr. *protos,* first), a nitrogenous substance found in the bodies of plants and animals.

proteus, *prō'tē us* (a sea god who had the power of assuming different shapes), the specific name of an ameba.

protoplasm, *prō'tō plazm* (Gr. *protos,* first; *plasma,* a thing formed), the essential substance of the bodies of organisms.

protopodite, *prō top'ō dīt* (Gr. *protos,* first; *pous,* a foot), the basal segment of a crustacean appendage.

Protozoa, *prō tō zō'ä* (Gr. *protos,* first; *zoon,* animal), a phylum of animals (see p. 80).

proximal, *prok'si mal* (L. *proximus,* nearest), situated near the place of attachment.

pseudopodium, *sū dō pō'di um* (Gr. *pseudes,* false; *pous,* foot), a temporary protrusion of the protoplasm in certain animals.

pupa, *pū'pä* (L. *pupa,* a doll), a stage in the life cycle of certain insects.

pyloric, *pī lor'ik* (Gr. *pulorus,* a gate-keeper), of or pertaining to the orifice between the stomach and the intestine.

pyrenoid, *pī rē'noid* (Gr. *puren,* the stone of fruit; *eidos,* form), a small colorless mass of proteid.

reaction, *rē ak'shon,* the response to a stimulus.

recapitulation, *rē ka pit ū lā'shon* (L. *re,* again; *capitulum,* a head), a theory that holds that the individual in its development passes through the ancestral stages of the race (see p. 228).

reduction, *rē duk'shon* (L. *re,* back; *ductus,* led), the halving of the number of chromosomes in the germ nuclei during maturation.

reflex, *rē'fleks* (L. *re,* back; *flexus,* bend), bent back (see p. 302).

regeneration, *rē jen e rā'shon* (L. *re,* again; *genero,* I beget), the renewal of a portion of lost or removed tissue.

respiration, *res pi rā'shon* (L. *re,* back; *spiro,* I breath), the absorption of oxygen and excretion of carbon dioxid.

rostrum, *ros'trum* (L. *rostrum,* a beak), a beaklike structure.

saltation, *sal tā'shon* (L. *saltatio,* dance), an abrupt transition or change.

saprophytic, *sap rō fit'ik* (Gr. *sapros,* putrid; *phytos,* a plant), living on decaying substances.

scaphognathite, *skā fog'nā thīt* (Gr. *skaphe,* a boat; *gnathos,* a jaw), a plate which bales the water out of the branchial chamber of the crayfish.

schizogony, *skī zog'ō ni* (Gr. *schizo,* I cleave), reproduction by splitting.

secretion, *sē krē'shon* (L. *secretus,* separate), the process of separating substances by glandular activity.

senescence, *sē nes'ens* (L. *senex,* old), the condition of growing old.

sensory, *sen'sō ri* (L. *sensus,* sense), capable of receiving or transmitting impressions from without.

septum, *sep'tum* (L. *septum,* a partition), a wall separating two cavities.

seta, *sē'tä* (L. *seta,* a thin, stiff hair), bristles, or stiff hairs.

sexual, *sek'sū al* (L. *sexus,* sex), of or pertaining to sex; done by means of the two sexes, male and female.

sinus, *sī'nus* (L. *sinus,* hollow), a cavity or hollow in tissue.

somatic, *sō mat'ik* (Gr. *soma,* body), of the body; applied to cells that do not take part in reproduction.

somite, *sō'mīt* (Gr. *soma,* body), a segment of an articulated body.

spermatid, *spĕr ma tid'* (Gr. *sperma*, seed), a cell which is converted into a spermatozoon.

spermatocyte, *spĕr'ma tō sīt* (Gr. *sperma*, seed), a stage in the maturation of a spermatozoon.

spermatogenesis, *spĕr'ma tō jen'ĕ sis* (Gr. *sperma*, seed; *gennao*, I produce), the origin and development of spermatozoa.

spermatogonium, *spĕr'ma tō gō'ni um* (Gr. *sperma*, seed; *gonos*, generation), a male germ cell just before maturation takes place.

spermatozoon, *spĕr'ma tō zō'on* (Gr. *sperma*, seed; *zoon*, animal), a mature male germ cell.

spireme, *spī'rēm* (Gr. *speirao*, wind round), the stage in mitotic nuclear division when the chromatin is in the form of a thread.

spore, *spōr* (Gr. *spora*, seed), a small reproductive body of certain animals.

statocyst, *stat'ō sist* (Gr. *statos*, stationary; *kustis*, a bladder), the organ of equilibration of the crayfish.

statolith, *stat'ō lith* (Gr. *statos*, stationary; *lithos*, stone), a solid particle within a statocyst.

steapsin, *stē'p'sin*, a ferment which resolves fats into fatty acids and glycerin.

sterile, *ster'il* (L. *sterilis*, barren), not reproducing its kind.

sternum, *stĕr'num* (Gr. *sternon*, the breast), the ventral part of a somite of an arthropod.

stigma, *stig'mä* (Gr. *stigma*, a mark), applied to spots of color, or to small openings.

stimulus, *stim'ū lus* (L. *stimulus*, a goad), something which evokes some functional or trophic reaction in the tissues on which it acts.

symbiosis, *sim bī ō'sis* (Gr. *sumbiosis*, a living together), the living together of two different species of organisms (see p. 297).

systole, *sis'tō lē* (Gr. *sustole*, a drawing together), the period of time during which a rhymically pulsating vessel is contracted.

telophase, *tel'ō fāz* (Gr. *telos*, end), the last phase of mitotic cell division, during which the nuclei are re-formed.

telson, *tel'son* (Gr. *telson*, the end), the last joint of the abdomen of the crayfish.

testis, *tes'tis* (L. *testis*, a witness), the male germ gland.

thermotropism, *thĕr mot'rō pizm* (Gr. *thermo*, heat; *trope*, turn), reaction to heat.

thigmotropism, *thig mot'rō pizm* (Gr. *thigma*, touch; *trope*, a turning), reaction to contact.

thorax, *thō'raks* (Gr. *thorax*, the breast), that part of the trunk situated between the head or neck and the abdomen.

tissue, *tish'ū* (L. *texere,* to weave), an association of similar cells with special functions to perform.

trachea, *trā'kē ā* (Gr. *tracheia,* the windpipe), a breathing tube of an insect.

trichocyst, *trik'ō sist* (Gr. *thrix,* hair; *kustis,* a bladder), a small hairlike structure of certain Protozoa (see p. 62).

triploblastic, *trip lō blas'tik* (Gr. *triploos,* threefold; *blastos,* a germ), having three germ layers.

tropism, *trō'pizm* (Gr. *trope,* turn), a turning caused by stimulus.

typhlosole, *tif'lō sōl* (Gr. *tuphlos,* blind; *solen,* tube), a thick fold of the intestine of certain annelids.

unicellular, *ū ni sel'ū lär* (L. *unus,* one; *cellula,* a cell), consisting of a single cell.

uniramous, *ū ni rā'mus* (L. *unus,* one; *ramus,* branch), having one branch.

uropod, *ū'rō pod* (Gr. *oura,* tail; *pous,* foot), the last appendage of the cray-fish.

uterus, *ū'te rus* (L. *uterus,* the womb), a special section of the oviduct.

vacuole, *vak'ū ōl* (L. dim. of *vacuus,* empty), a minute vesicle in certain Protozoa.

vagina, *vā jī'nā* (L. *vagina,* a sheath), the passage leading from the uterus to the genital orifice in certain females.

ventral, *ven'tral* (L. *venter,* the belly), of or pertaining to the under side of the body.

vitalism, *vī'tal izm* (L. *vita,* life), a biological doctrine (see p. 24).

zoology, *zō ol'ō ji* (Gr. *zoon,* animal; *logos,* discourse), the science of animals.

zygote, *zī'gōt* (Gr. *zugon,* a yoke), the body formed by the conjugation of two gametes.

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